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ALLEE MEMORIAL NUMBER: INTRODUCTION

Ever since 1920 the study of animal behavior has been increasingly concerned with the problem of social organization in animals, and there has been increasing pressure and enthusiasm for providing the material for a basic science of general sociology which will provide a scheme of reference for the study of human behavior from a social and ecological viewpoint. One of the greatest needs is for comparative studies of social behavior with which to furnish an adequate descriptive basis for general theories.

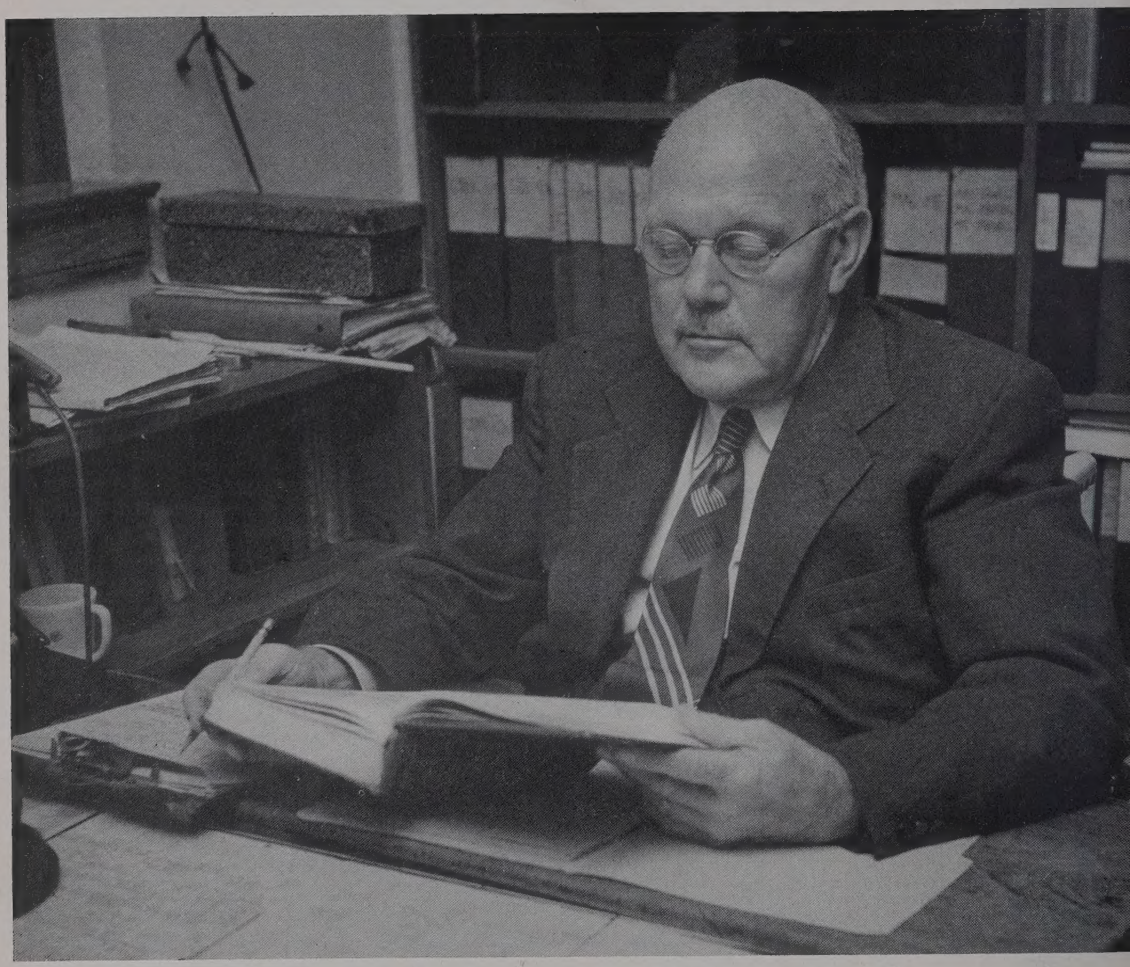
With this in mind, the Editorial Board devised the plan of publishing a group of representative papers involving various aspects of animal behavior so that this particular aspect of ecology might be presented as a unit rather than as scattered papers with no apparent connection. The result is presented here as an experimental venture with the idea that similar groups of papers on other aspects of ecology might be published from time to time.

The method of selecting the papers was to write the members of the Ecological Society's Committee on Animal Behavior and Sociobiology and ask them to either contribute current research or to nominate someone else who had important research material available and ready for publication. The group of papers does not include every important aspect of present-day research, but it can be said to be a fairly representative sample of research being carried on in the United States, where workers have tended to analyze whole societies and populations. A corresponding group of European papers would probably put more emphasis on the study of specialized patterns of behavior and their evolutionary significance.

The first group of papers is concerned with the general problems of social organization. The paper by Scott outlines the systematic procedures whereby animal societies can be described and compared. There follow three papers which illustrate portions of these general techniques. The paper by King is a systematic study of the social behavior patterns of *Cavia* under seminatural conditions as a basis for understanding the social organization of related wild species. The paper by Collias is on the important subject of socialization, the process by which social animals, early in life, tend to form positive social relations with one group of animals and to prevent such relationships being formed with others. Collias' paper does much to dispel the mystery which has surrounded this process and indicates that an explanation can eventually be found in the combined action of endocrine and psychological factors. The paper by Banks is an excellent example of the analysis of specific social relationships. He finds that the dominance hierarchy of the Indian jungle fowl and the associated behavior patterns are essentially similar to those of the domestic fowl. This indicates that neither environment nor selection have essentially altered the behavior of chickens and it may be concluded that the dominance order is more than a product of domestic conditions.

Another great problem in animal behavior is that of establishing the ecological and physiological basis of adaptation and social behavior. The paper by Emerson is an experimental field study on the adaptive value of nest building in the termite which supports the view that social behavior may have the function of providing a stable environment. The paper also illustrates the fact that good experiments can be done under field conditions. There is still a great need for thorough descriptive studies of animal behavior under field conditions, particularly in species which have been relatively undisturbed by man. These studies are difficult to do because of expense and personal inconvenience, but such studies have made some of the outstanding contributions to the field.

The paper by Christian includes material relating to one of the important new approaches to population problems. Students of social behavior have long appreciated the fact that there is very seldom actual competition between the adults of social species, particularly if they belong to a natural social group. This paper indicates that in some species numbers may be controlled partly by infant mortality and partly by physiological reactions controlling fertility under conditions of high population pressure. The paper by Weise is another link in the evidence which is piling up



Warder Clyde Allee
1885-1955

around the problem which Rowan labelled the "riddle of migration." Both external stimulation and internal physiological conditions seem to affect the tendency of the bird to become restless and migrate.

The final paper by Calhoun is a behavioral analysis of the phenomenon of home range in rodents. Where mice react to a particular goal such as shelter or food they are likely to travel only as far as the nearest available source of satisfaction. However, in their exploratory behavior they are likely to travel considerably farther until some limit is reached. It may be inferred that the results of trapping data based on food or shelter boxes might tend to give a somewhat limited picture of the true home range.

It seems particularly appropriate that this group of papers, and the number of ECOLOGY whose animal half it comprises, should be dedicated to the memory of Warder Clyde Allee, pioneer student and tireless investigator of animal behavior.

J. P. SCOTT

THE ANALYSIS OF SOCIAL ORGANIZATION IN ANIMALS[1]

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INTRODUCTION

Following Darwin's emphasis on the principle of adaptation in organic evolution, biologists became strongly interested in the study of individual animal behavior. Adaptation could only be inferred from fossils, but could be observed directly in living forms. Up till 1900 a great many biologists concentrated their efforts in this field, which was at that time almost as popular as comparative anatomy and embryology. Shortly afterwards two discoveries were made which strongly influenced this type of research. One was the rediscovery of Mendelian heredity, and a great many workers who were interested in general evolutionary problems shifted their attention to genetics. The other was the establishment of general laws of learning following Pavlov's studies of conditioned reflexes, and those workers with psychological interests tended to elaborate these finding with studies of behavior in the rat.

About 1920 a new era in behavioral research began with the description of social organization in birds. Elliot Howard (1920) wrote on the significance of song and territory in birds and Schjelderup-Ebbe (1922) discovered the existence of social dominance in chickens. Shortly afterward Allee appoached the problem from a more general viewpoint with his review on animal aggregations (1927) and later book by the same title (1931). Since that time a large body of information has been accumulating around the problem of social organization, and this paper will briefly describe some general methods and the kinds of results to be expected from its study.

[1] This paper was originally delivered, September 7, 1954, at Gainesville, Florida, as part of a program on "Social organization of Animals" given in honor of Dr. W. C. Allee.

The study of the social organization of a species may be delimited by the natural units of social organization, which are usually species populations and their subgroups. It differs from a general ecological study in which the unit of organization is the animal and plant community, which may be composed of many different sorts of animal and plant populations. It also differs from psychological analysis in which the unit of organization is the individual and where the primary interest lies in internal organization. So defined, the analysis of social organization occupies an intermediate position between the sciences of ecology and psychology, and overlaps with both at many points.

At the present time we have only a few definite standard techniques for the study of social behavior and organization (Scott, 1950). However, there are certain general methods which have achieved wide use and which can be recommended to anyone working in the field. The analysis of social organization in any animal should begin with a thorough descriptive study in which the seasonal and daily cycles of behavior are thoroughly surveyed. An essential part of this study is the identification of individuals, since without this information the details of social organization can only be surmised. Descriptive study should also include a study of the development of social behavior and organization from birth to maturity, since behavior and organization change with age. This systematic descriptive information naturally leads to certain hypotheses which can be studied experimentally, and it is found that many types of factors can affect social organization. These may be described as ecological, psychological, physiological, and genetic; and appropriate techniques used for the examination of each.

Classification of General Behavior Patterns and Their Comparative Study

In relating genetic factors to social organization it has been found that each species has certain characteristic ways of adapting to the environment and that these "patterns of behavior" in part determine the nature of social organization which can be developed in the species. As a guide to the study of characteristic patterns of behavior the author has developed a general scheme of classification. This scheme is intended to include the kinds of behavior generally recognized by students of animal behavior rather than to conflict with them, and has been found useful in making general descriptive studies of the type described above (Scott 1945, 1950a). It was developed originally by attempting to classify the behavior patterns described in several species of animals by other authors, as in Allen's (1911-1914) study of the blackbird and Dean's (1896) study of the river dogfish.

The chief rule for any good scheme of classification is that it should be natural and conform to discontinuity which exists in nature and which can be recognized by independent observers. The scheme of classification should be logical, and one which includes all related phenomena. Terms in common usage may be employed, provided their meanings are clear and describe the observed phenomenon correctly, but they should not be redefined with new meanings as this leads to great confusion. Finally, terms should be descriptive and not imply some theoretical interpretation of the facts.

These rules for classification and terminology conform to general usage in biological science. In addition, the author feels that one should be conservative about forming new terms inasmuch as they add to the labor of acquiring a scientific vocabulary, but that one should not hesitate to form new ones where necessary. Those which are useful will stand the test of time and those which are not useful will tend to be discarded.

The following classification includes all the major patterns of social and semi-social adaptation which have so far been described.

Contactual Behavior. This may be defined as simply maintaining bodily contact and, as Allee (1931) has shown, the formation of simple aggregations through behavior of this sort occurs very widely throughout the animal kingdom. The adaptive significance of the behavior may vary a great deal. A group of mammals may huddle together for warmth whereas a group of Paramecia may form because the bodies of their fellows afford protection against unfavorable chemical conditions. This extremely simple type of social behavior affords a possible basis for the evolution of higher types of behavior.

Ingestive Behavior. This may be defined as behavior concerned with the taking of solids and liquids into the digestive tract and is found very widely although not universally throughout the animal kingdom. It may have an important social significance in animals which feed their young, and becomes highly social in the nursing behavior of mammals.

Eliminative Behavior. This is defined as behavior associated with the elimination of urine and feces from the body. Special behavior is rarely seen in aquatic animals but highly elaborate patterns may be developed in terrestrial species which build nests or lairs. In such forms as wolves and the prong-horned antelope, it may acquire considerable social significance.

Sexual Behavior. This may be defined as behavior connected with the fertilization process and includes the usual courtship and copulation behavior of animals. It occurs very widely though not universally in the animal kingdom and is undoubtedly one of the most primitive forms of social behavior.

Epimeletic Behavior (Gr. *epimeleteon,* caregiving). This may be defined as the giving of care or attention. It has been called maternal behavior but is also found in males in animals like the ostrich which incubates the eggs, and in many other animals where there is biparental care of the young. It could be called parental behavior except for the fact that in many species it is done by animals other than the parents as, for example, the mutual grooming of adult primates, and the care of the young by worker females in the social insects. This behavior includes what has been called by the more specific terms of attentive behavior and nurturance.

Et-epimeletic Behavior (Gr. *aeteo,* beg, + epimeletic). This is defined as calling and signaling for care and attention and is very widely found in animals which give some care to the young. The behavior may be vocal, as in infant mammals, or simply be some sort of movement, as in the larvae of bees and ants. This behavior could be called infantile except that it also occurs in adult animals. In most cases it is used as a substitute for direct adaptation by an individual which is itself helpless or unable to adapt.

Agonistic Behavior (Gr. *agonistikos,* combattive). This is defined as any behavior associated with conflict or fighting between two individuals. The term fighting behavior was originally used, but it was found that patterns of behavior involv-

ing escape or passivity were very closely related and could not be included under the narrow term of fighting. This type of behavior occurs principally in the arthropod and vetebrate phyla.

Allelomimetic Behavior (Gr. *allelo,* mutual, + *mimetikos,* imitative). This is defined as any behavior in which animals do the same thing with some degree of mutual stimulation and consequent coordination. It is seen developed to a high degree in schools of fishes, flocks of birds and herds of mammals. It could be called imitative behavior except that to most people this implies some degree of learning, which is not necessarily involved, and the idea of a model and a mimic rather than mutual stimulation. Such behavior in birds has been described as mimesis by Armstrong (1952) and as contagious or infectious behavior by other authors. The two latter terms appear to be somewhat undesirable in that they suggest that the behavior is transmitted in the manner of a disease.

Investigative Behavior. This may be defined as sensory inspection of the environment. This has been called exploratory behavior in the rat, where the animal actively explores the environment with nose and whiskers. However, in an animal with highly developed eyes, such behavior may consist merely of glancing around without movement of the whole body. The more general term of investigation appears preferable.

When the above classification is used to organize descriptive data the result is a detailed list of activities under each category which gives the characteristic ways in which a species responds in relation to major behavioral functions (Scott 1950a). Many of these exist in playful or immature forms as well as adult patterns.

It is also possible that patterns of behavior grouped in the above or similar categories may reflect an underlying nervous organization. For example, the behavior of an inexperienced male mouse of the C57 Black strain attacked by a superior fighter follows a regular and predictable sequence (Scott and Fredericson 1951). He first fights back, and when this is not successful he attemps to escape. If he fails in this he adopts a defensive posture, and if cornered he may lie on his back with feet in the air. We may eventually come to think of "systems of behavior" organized around a particular function, but general evidence still needs to be obtained on the point.

The categories may also be used to check the completeness of a descriptive study, leading to the discovery of behavior which has passed unnoticed. Sometimes a major category of behavior is almost or entirely absent, and this affords an opportunity for characterizing the social life of the species. For example, allelomimetic behavior is highly developed in the sheep and almost entirely absent in the mouse, which results in two very different types of social organization (Scott 1945a).

Species differences can also be found within a category of behavior. For example, the agonistic behavior of sheep and goats consists largely of butting. Sheep back off and run together head on, but goats typically rear up and butt with a sideways thrust of the head. A scheme of classification can be used as a systematic framework for such comparative studies of species differences in behavior, as well as making it easier to do a complete descriptive job. A high standard of scholarship requires such a complete systematic method, which has too often been missing in past studies of comparative behavior.

Comparative studies lead to the conclusion that the presence or absence of a given type of social behavior affects the type of social organization developed by the species. Stated more specifically, the presence of a given behavior pattern defines the types of social relationships which may be developed from it.

Social Relationships

Social organization may be analyzed in terms of social relationships. Such a relationship is defined as regular and repeatable behavior between two or more individuals, and it in turn may be described in terms of the patterns of behavior exhibited by the individuals taking part. The classical example of a social relationship is the peck order in hens in which one individual regularly threatens or pecks the other which just as regularly dodges or submits to pecking. Social behavior is not identical with social organization. In the case of two strange hens, behavior at first consists of unorganized fighting, and it is only after several encounters that behavior is organized through learning and habit formation into a regular dominance-subordination relationship. Even in the social insects, where heredity seems to play a relatively stronger role, social organization is not automatic. Experience in early life determines the species with which social relationships are formed by larvae taken by slave-raiding ants. Social behavior may therefore be considered an important but not the sole determiner of social relationships, and this should be kept in mind in making analyses of the two phenomena.

A great many types of social relationships are theoretically possible if all types of social behavior are considered. The number of possible combinations of behavior patterns in a species which shows all of the 9 types of behavior classified above may

be theoretically calculated as follows. There are 9 possible combinations where both members of the relationship exhibit the same type of behavior and 36 possible combinations where the individuals exhibit unlike behavior, making a total of 45 (Scott 1953). Some of these combinations are frequently seen, such as the dominance order in which behavior of both individuals is agonistic. Some of them may be commonly overlooked as, for example, the combination of sexual and agonistic behavior exhibited by male and female rodents when the female is not in heat, and many of them are yet to be described. It is possible, of course, that certain ones are only theoretical and do not occur in nature. Some of them which have been widely observed are described below, using the names commonly applied to them.

Simple Aggregations. In this type of relationship the behavior of both animals is contactual. As Allee has shown, such relationships exist very widely in the animal kingdom, but their occurrence is apt to be irregular and nonspecific because of their dependency on environmental conditions.

Dominance-Subordination Relationships. In this type of relationship the behavior of both individuals may be described as agonistic. That of one individual consists of a threat or actual fighting while the other individual remains passive or attempts to escape. Evidence gathered by Allee (1950) and his students and summarized by Collias (1944) shows that this type of relationship is widespread in the vertebrates and occurs in at least some arthropods. It does not occur in many of the lower animals which are incapable of fighting.

Leader-Follower Relationships. The behavior of both individuals may be classed as allelomimetic, but there is an unequal degree of stimulation so that one tends to lead and the other follow. This has been described in sheep (Scott 1945), deer (Darling 1937) and ducks (Allee *et al.* 1947) and deserves more extensive study. It should not be confused with cases in which a dominant animal drives a group before him, as in the case of a stag and does in the rutting season.

Sexual Relationships. The behavior of both individuals is sexual. Although sex behavior has been extensively described in many species, very few analytic studies of the resulting social relationships have been made. Dominance and sexual relationships may be interdependent in both chickens (Guhl and Warren 1946) and chimpanzees (Nowlis 1942).

Care-Dependency Relationships. In this case the behavior of one individual is epimeletic while the behavior of the other individual may be one of several different types. An infant animal may exhibit et-epimeletic behavior, as when a young lamb is separated from the flock, or it may exhibit ingestive behavior in the process of nursing. In animals like dogs which regularly clean the young, the latter may exhibit eliminative behavior. This type of relationship has been widely described but subjected to very little experimental analysis in animals.

Mutual Care. In this case the behavior of both individuals is epimeletic, and an example is seen in the mutual grooming of primates. In spite of its theoretical importance for considerations of basic human sociology, such relationships have been little studied in animals.

Trophallaxis. This is a complex relationship described by Wheeler (1923) in the social insects. Both individuals may exhibit investigative behavior, and one usually exhibits epimeletic behavior in providing food from the crop while the other ingests the food. On subsequent occasions the roles may be reversed.

Mutual Defense. This is another complex relationship in which the members exhibit both agonistic and allelomimetic behavior. It has been described in such animals as muskoxen, wolves, baboons and many kinds of birds in reaction to hawks, but has not been subjected to extensive analysis.

It would appear from the above presentation that the complete analysis of the social organization of a species can be an extremely complex affair, and that the simple description of the dominance-subordination relationships does not give the whole story by any means. However, the task is not hopeless since in any actual case the number of important relationships turns out to be relatively small.

Biological Classification of Social Relationships

As described above, analysis of the social organization of an animal species consists of a systematic description of the basic patterns of behavior and their organization into social relationships. If an animal gave the same responses to all individuals the relationships would be simple to describe and a low degree of social organization would result. As indicated above, the behavior of individuals is frequently unlike and the concept of differentiation (Tinbergen 1953) becomes a useful one. Behavior may be differentiated by biological factors such as age and sex on the one hand and by psychological factors involving learning on the other. As Carpenter (1934) has pointed out, there are three biologically determined types of individuals in mammals: males, females and young.

When these are combined in all like and unlike combinations, a total of six basic relationships can be established. These are essentially super-categories under which those relationships mentioned in the previous section may be grouped. For example, male-male relationships can include dominance-subordination and mutual care relationships as well as many others. This general scheme can be applied to other animals as well as primates and is particularly useful in studying groups of wild animals where it is difficult to distinguish individuals except by age and sex.

In the case of the social insects which have biologically differentiated castes, the scheme may be amplified to include greater numbers of basic relationships. A similar extension must be made when social relationships are developed between two different species, as commonly occurs in domestication (Scott 1953).

Analysis of Specific Social Relationships

So far, the analysis of social organization has been considered in terms of behavior of the whole organism and relationships between organisms. It is also possible to investigate the internal processes which in part determine behavior and through it influence social organization. Since the methods used are well known to physiologists and psychologists, the scope of such investigations will be described only briefly here.

One basic field of study is the analysis of the complex network of physiological factors which is associated with any major pattern of behavior (Scott and Fredericson 1951). Available information of this sort tends to be scattered and unequal. The physiology of sexual and ingestive behavior has been widely studied, but our knowledge of agonistic behavior comes largely from the domestic cat. The physiology of certain types of behavior, such as investigative and allelomimetic, is almost completely unknown.

A related field of investigation is concerned with the physiological genetics of social behavior and social relationships. As Collias has shown (1943), dominance-subordination relationships may in part be determined by such physiological factors as weight and hormones, which in turn may depend on the genetic differentiation of sex. Further genetic variability in physiological factors affecting social behavior introduces an individual specificity into social relationships. Those of the genetic variant will fall into the usual broad categories but will also show certain unique and specific differences.

In animals which are capable of learning, social behavior becomes differentiated on the basis of mutual adaptation and habit formation as well as on the basis of biological differences. As shown by Ginsburg and Allee (1942) the formation of a dominance order is at least in part related to the psychological principles of learning. Once such a relationship is formed and firmly established by habit, it may be extremely difficult to upset it by altering biological factors, as shown by Beeman and Allee (1945). Among the higher animals it is probable that all social relationships are affected by the psychological processes of problem solving (or adaptation) and habit formation. Neglect of these factors in favor of an assumption of purely genetic or instinctive determination of behavior may lead to serious errors of interpretation (Lehrman 1953).

As with physiological factors, psychological processes tend to introduce specificity into social relationships. In a study of social organization of sheep it was found that any given lamb had a general leader-follower relationship toward all adults in its tendency to follow them, although this tendency was strongest with regard to the mother. Its care-dependency relationships, on the other hand, were extremely specific and developed only with its own mother (Scott 1945).

In any species which has the psychological capacity to discriminate between individuals, such specific relationships will be expected to occur. It likewise follows that unless the scientific observer develops a similar ability to identify individuals, specific social relationships will pass unnoticed, and with them a large part of social organization. There is a vast difference between the observation that hens tend to peck each other (a general relationship) and the knowledge that within each pair there is one which always pecks and one which always dodges (a peck order consisting of a group of specific relationships).

If social relationships were entirely determined by biological factors it would be expected that all female-female relationships in a given species would be the same except as affected by chance genetic variability. Such is obviously not the case in the peck-order studies, and it is probable that a similar specificity will be found in many other types of social relationships when studied in detail. The general analytic method is to identify all individuals in the social group and then bring them together in pairs in a situation which will elicit the kind of behavior being studied (agonistic, sexual, etc.). A well-designed experiment includes results on all possible combinations of pairs, observed in an order which controls factors such as fatigue, habit formation, etc. The total possible number of combintions in a group is given by the

formula $\frac{n(n-1)}{2}$ (Carpenter 1940), so that such a study becomes very lengthy if n (the total number of individuals in the group) is large. The study should be supplemented with observations on the whole group, as it is possible that pairs may react differently when in the presence of others.

Many models for this type of study may be found in the literature (Collias 1951), particularly those done with dominance-subordination relationships, and the methods need not be described in greater detail here. Guhl (1953) has written an excellent summary of methods used for the study of specific dominance and sexual relationships in the domestic fowl. As indicated above, there is a need for the extension of these methods to the study of other sorts of social relationships in order to obtain a more complete picture of social organization.

The importance of specificity in social relationships is likewise apparent when analysis is made from a developmental viewpoint, and this has led to the concept of socialization.

Socialization

Experiments which modify the social environment have tended to bring out the general principles of socialization. Any highly social animal that has been so far studied has behavioral mechanisms whereby, early in development, an individual forms positive social relationships with its own kind and usually with particular individuals of its kind. At the same time, other behavioral mechanisms operate to prevent such relationships being formed with other species and, to a lesser extent, with other groups of its own kind. Raising an individual with any other species including human beings usually produces an individual which is socialized to the strange species. Essential patterns of social behavior remain unaltered and are given in response to the strange species to the extent that such behavior is compatible.

The process of socialization has been shown to take place within limited periods of time by Lorenz (1935) in birds and also in such mammals as the sheep (Collias 1953) and dog (Scott and Marston 1950). Lorenz has been chiefly concerned with the positive mechanisms to which he has given the general term "imprinting," but, in the case of the mammals mentioned, some information is also present regarding the negative mechanisms which normally prevent social attachment to other species. In the dog and wolf, for example, agonistic behavior may be elicited by strangers at a very early age, effectively preventing positive contact as the animal grows older (Scott 1953a).

These effects have led to the concept of critical periods in the process of socialization (Scott and Marston 1950). There are points in development where it is very easy to change the individuals to which an animal becomes socialized, and other points later or earlier in development when this is difficult or impossible. A study of the process of socialization thus forms an important part of the developmental analysis of social organization.

An excellent review of experiments on the general effects of modifying early experience has been made by Beach and Jaynes (1954). As applied to the problem of social organization the most useful techniques may be outlined as follows. The first step is a detailed descriptive study of development, paying particular attention to social behavior patterns and changes in sensory, motor and psychological capacities. We have attempted to set up a model outline for this type of study in the case of two species of mammals, the dog and mouse (Scott and Marston 1950; Williams and Scott 1953).

A developmental study may be supplemented by two sorts of simple experimental procedures. One is to take male and female individuals at birth or hatching and have them reared by another species, human or otherwise. This method has produced brilliant results in the hands of Lorenz (1935), and may be extended further to the rearing of individuals in semi-isolation (Thompson and Heron 1954). The other is to castrate male and female individuals as early as possible in development, which gives some indication of the importance of hormonal changes and sexual behavior in social development.

Observations on the time of development of various capacities and patterns of behavior require experimental verification. On the basis of present evidence, the development of many species falls into natural periods based on beginnings or changes of important social relationships. This gives a basis for the experimental analysis of the factor of time in early social experience. Modification of social experience may be begun at different points in development and continued for appropriate periods. Controls for physiological and structural changes, genetic differences, random environmental factors and the psychological factors of learning are important in the design of these experiments (King and Gurney 1954).

Social Organization between Groups

Most of the work on analysis of social organization has been done within groups, and correctly so. The most frequent aspects of social life in animals appear to be concerned with what are called by the human social psychologists "face-to-face

contacts in small groups." However, some organization between groups apparently does exist, as reported in Carpenter's (1934, 1940) studies of howling monkeys and gibbons. Likewise, the territorial organization of passerine birds during the breeding season may be considered as organization between small family groups. Obviously, such organization is most likely to occur under natural conditions, and its existence is one of the possibilities which should be looked for in field studies.

The evidence for the existence of territoriality in small mammals has been summarized by Blair (1953), who finds that instances of defense of definite boundaries are relatively rare. As with birds, group territorial defense in mammals may be described simply in terms of a general dominance-subordination relationship, in which the group or individuals within the group tend to be dominant over the individual trespassing on the territory (Murie 1944; King 1955). However, in the case of howling monkeys Carpenter (1934) reports that groups maintain regular daily contacts with each other by howling at dawn, and this is possibly also the case in birds such as quail which vocalize regularly. The "wars" between colonies of ants appear to involve a general relationship in which all strange individuals are attacked.

The relationship between separate social groups is a problem of considerable theoretical interest and should be investigated wherever possible. Analysis should include the means by which new groups are formed, and the fate of isolated individuals as well as territoriality. King (1955) has found a definite group territorial system in prairie dogs, with a tendency for adults to move out and colonize new areas after raising the young, which are left to occupy the old territory. Carpenter's (1940, 1934) studies of the gibbon and howling monkey are excellent models for the analysis of this and other aspects of social organization.

Conclusion

It will be seen from the foregoing outline that the complete analysis of the social organization of even a single species is an enormous task. It is not likely that the job will ever be entirely completed, though such a point is being approached in such favorite objects of study as the chicken, mouse, stickleback, honeybee, army ant and termite. The task must be divided into sections, and emphasis placed upon important points of fact and theory.

Collecting observations on behavior patterns and their organization into basic biologically determined social relationships can often be done with a study of a year or two. Much material is already available in publications written for other purposes, particularly in natural history and ecological life history studies. A great deal of information on European species is contained in studies of comparative behavior patterns done by the "ethologists," although they have frequently concerned themselves with the nature of stimulation ("releasers") rather than social organization. The systematic classification of material from these sources often saves a great deal of time as well as providing confirmatory evidence for original study.

The analysis of socialization and specific social relationships is more complicated and time-consuming, and is difficult to do except in laboratory or semi-natural environments, although it has been shown that social dominance does exist under natural conditions (J. W. Scott 1942). Indeed, the more basic the analysis, the slower it becomes, and a division of labor among scientists is necessary when physiological and genetic factors are studied. This brings up the problem of coordination of effort.

The study of the social organization of behavior tends to unify knowledge. Behavior is usually defined as activity of an entire organism and thus is affected by factors customarily divided up in all the conventional subdivisions of zoology and psychology. When behavior is considered in relation to social organization the subject matter is widened still further to include certain aspects of general social science. It is obviously impossible for anyone to have a thorough and complete knowledge of all these fields, but the specialist in any one of them should at least have a general knowledge of the others and their relation to his own. The ecologist, as a last surviving type of general biologist, should have a particular advantage in this respect. Meetings such as this one, in which the speakers have training in such diverse fields as genetics, psychology, and ecology, can do much to promote the interchange of ideas and mutual comprehension.

A final word may be said concerning the necessity of maintaining a high standard of scientific work. As stated in the beginning of this article, we still have very few specific standardized techniques for the analysis of social organization, and to insist upon the enforcement of standards prematurely would do much to discourage new and creative lines of research. The harm that can be done by publishing inconclusive pilot experiments or generalizing from superficial descriptions based on study of a few individuals is equally great. We can and should insist on general standards of thoroughness and repeatability, on controls for the wide variety of genetic, physiological, developmental, psychological, ecological, and social factors

known to affect behavior, and on the necessity for final experimental verification of any theory.

The resulting well-established facts and theories of social organization in animals have widespread significance. Such information has great practical importance in wildlife management and in the care of animals under domestication. For example, if it is planned to recolonize a vacant territory with social animals, the new individuals must have been socialized toward each other or otherwise the group will disintegrate and fail to survive.

A knowledge of social organization is an essential part of understanding the general ecology of the species. Populations of animals do not exist in nature as randomly distributed individuals but as socially organized groups. Enough has been said in the foregoing article to indicate that an immense amount of information is still to be gathered about the social organization of animals, and even some of our common and familiar species are far from completely understood.

Finally, the collection of knowledge regarding social organization in animals and the resulting generalizations which will be made should prove to be of great help in understanding certain human problems. A great many problems of human maladjustment can be attributed to interference with the process of socialization, whose study should be one of the primary concerns of child psychology. A more thorough knowledge of animal societies should contribute greatly to our understanding of the biological and psychological bases of human social organization.

Summary

An attempt has been made in this article to present a systematic general outline for the analysis of social organization in animals. Methods include systematic description of the important behavior patterns of the species based on studies of the daily and seasonal cycles of behavior and upon the development of behavior in the individual from birth until maturity and old age. These basic patterns of behavior determine to a large extent the general types of social relationships which are possible in the species.

Further analysis of specific social relationships depends upon identification of every individual in the social group and should be verified by experimental combinations of every possible pair.

Study of the process of socialization should include a systematic descriptive study of changes in the basic behavioral capacities: sensory, motor, psychological, and patterns of social behavior, with particular reference to relative timing and its consequences. Some remarks are made concerning general application of the method, and the significance of the results.

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SOCIAL RELATIONS OF THE DOMESTIC GUINEA PIG LIVING UNDER SEMI-NATURAL CONDITIONS[1]

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INTRODUCTION

A comparative study of mammalian societies is often limited by the difficulty of observing wild species in their native environments. The mammals may be nocturnal, secretive, or they may live in inaccessible habitats, which prevent ready observation of their social behavior. In order to fill the gaps in a systematic study of social behavior, it is therefore necessary to employ techniques which permit the formulation of some concept of the social structure in noctural or secretive species. One technique is the study of wild species in the laboratory under semi-natural conditions or under artificial conditions. This technique necessitates a distinction between the social behavior of those individuals taken from their native habitats and studied directly, and those raised from infancy in captivity. Another technique is the study of domestic mammals under semi-natural conditions. This technique has the limitation that most domestic mammals are morphologically and socially different from their wild relatives.

The social behavior of a species may be modified by domestication. Both genetic and acquired patterns of social behavior undergo changes due to artificial selection, reduction of natural selection, and disuse. Consequently, a domestic species retains those social characteristics which are selected for under the conditions imposed by domestication and those which are least affected by the new environment. The conditions imposed by domestication of the cavy, for example, probably enhanced the survival value of social tolerance, while domestication had little effect on other social traits. The absence of close selection for social behavior in the cavy during its domestication should insure the preservation of many social characteristics of its progenitors. In a semi-natural environment, these basic patterns of social behavior should be exhibited by the domestic guinea pig and may be comparable to closely related wild species.

In the present report, the known information on the life history of several wild species of Cavia is compared with that of the domestic Cavia living under semi-natural conditions. This comparison should serve to give a reasonable estimate of the basic social patterns developed by rodents at the phylogenetic level of the cavy.

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The cavy belongs to the suborder of hystricomorphs, which include many of the South American rodents and whose only North American representative is the porcupine. The genus *Cavia* belongs to the family of Caviidae, which includes the following other genera: *Dolichotis*—large Patagonian cavies, *Kerodon, Galea,* and *Microcavia*—mountain cavies (Simpson 1945). The number of living species of the genus *Cavia* is uncertain; however, at least eight have been recognized (Thomas 1917). Recently Gilmore (1952) stated that he believed them all conspecific with *Cavia aperea.* Some support for this thesis is found in the breeding experiments conducted by Detlefsen (1914), Nehring (1893), and Castle and Wright (1916) who have shown that all forms tested in the laboratory are interfertile with the domestic guinea pig (*Cavia porcellus*), although some of the F_1 offspring are sterile. Because of this confusion concerning the taxonomy of the genus, I will refer to the wild forms of cavies by the specific names used by the various authors contributing to the knowledge of the animals' behavior.

Wild Cavies

Habitat and Food. In their native habitat, cavies subsist on fresh green vegetation and fruits. Wild *C. cutleri* have been observed in rock piles near irrigated fields and in the rock walls of cattle corrals located near an alfalfa field (Castle and Wright 1916). They are particularly fond of alfalfa. In brush country, they run with facility and rapidity for short distances to their caves which have many entrances among the lower branches of shrubs (Cabrera and Yepes 1940). *C. musteloides* make their burrows in ditches, stone walls or culverts along the roads, although many have their dens on the open plains, where they may live in the tunnels dug by the gopher-like tuco-tucos (Pearson 1951). In general, cavies are poor burrowers and depend upon naturally formed crevices or tunnels dug by other animals for shelter.

Behavior. Very little is known of the behavior of cavies in the wild, where they are only seen scurrying from one hiding place to another. *Cavia musteloides* is diurnal, appearing from the burrows well after dawn and returning to them about sunset (Pearson 1951). Gilmore (1952) remarks that these cavies are sedentary, gregarious without social organization aside from the usual male dominance over several (up to a dozen) females, accompanied by bitter fights between males.

In captivity, wild-caught and captive-born offspring of *C. cutleri* react alike, being very secretive, burrowing under hay when a human observer approaches (Castle and Wright 1916). They are extremely savage towards each other and no more than two may be raised together. Males will not live peacefully together under any circumstances and if more than one female is placed in a cage with a male, the other female severely persecutes it. Even young as they mature are not tolerated by the parents. *C. rufescens* are also fighters, which makes their breeding in captivity difficult (Detlefsen 1914). Male *rufescens* offered tame *porcellus* females "harassed and bit the tame females almost beyond recognition." Breeding male *rufescens* to tame female *porcellus* could only be done by keeping the male isolated for a time and then placing a female which had just given birth to young with him. In contrast, Nehring (1893) found little difficulty in rasing *C. aperea* in captivity.

Reproduction. The gestation period of *C. cutleri* is between 60 and 70 days or about 3 or 4 days shorter than *porcellus* (Castle and Wright 1916). The number of young per litter in Castle's captive colony varied from 1 to 4, with an average of 1.89 young to a litter. Births in captivity occurred throughout the year which is believed to be the case in the wild. Females may breed as early as two months of age, when less than half-grown. Full growth is attained in a year. The age of the oldest female that reproduced in captivity is estimated to have been 32 months. Males do not breed until at least 3 months of age, but may continue to sire young until they are 4 years old. Females have a postparous estrus.

A Guinea Pig Colony

The purpose of this experiment was to learn what adaptations the domestic guinea pig would make to its biologic and social environment under semi-natural conditions.

Description of Environment. A 2500-sq. ft area of open field was enclosed by a fence made of chicken wire about 1 ft high. Vegetation in the field stood approximately 1 ft high. Four huts, 18 in. by 12 in. by 8 in., were placed in each corner of the enclosure 8 ft from the fence. Oats were available to the guinea pigs in crocks located near the huts. A month after the inception of the experiment, during a drought, water was supplied near each hut. Water was supplied to the animals until freezing weather arrived. In order to facilitate observations the grass and weeds from three quadrants of the field were cut to a level of 4 inches. One quadrant was left unmowed. Late in the fall when the grass had been eaten by the guinea pigs and killed by the frost, some carrots and green vegetables were supplied.

Animals. A male and two pregnant females of each of three races kept at the Jackson Laboratory

were placed in three of the huts. The races were readily distinguishable by the colors. One race was white, another red, the third multi-colored. Individuals within a race were marked with fur dye in order to facilitate identification. All descendants of these 9 original animals are included in the study.

Collecting Data. Observations of the guinea pig colony began June 25, 1952 and continued throughout a year; however, most data used in this report were collected during the first four months.

Each day all of the animals were examined and weighed to the nearest ounce. During the first three weeks of the experiment they were kept in their huts at night and allowed out only during the day. Due to a considerable initial loss of weight, it was decided to give them freedom both at night and through the day. The hut in which each animal was found when weighed each day was also recorded in order to ascertain the voluntary groupings. Observations were first made at intervals throughout the day from a barn loft which overlooked the field. Later observations were made at 9 A.M. and 4 P.M. when the animals were more active than in the middle of the day.

Results

Relations to Environment. All nine original animals were laboratory-raised, so when they were placed in the field it took them some time to adapt to their new environment. This is indicated by their initial weight loss, mortality, and failure to utilize the entire field. The decrease in the biomass of the entire colony is shown in Figure 1 which includes only the original animals and their descendants. Because of the initial mortality, the female that died in the first week was replaced by another pregnant female which was not included in the biomass (Table I). It was not until the seventh week after the inception of the experiment

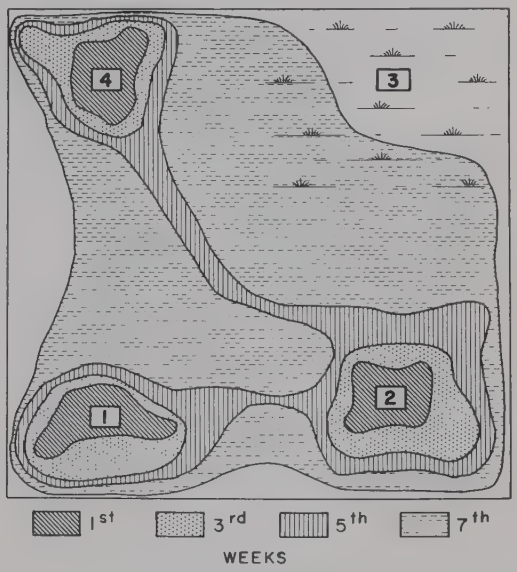

Fig. 2. Experimental field of 2,500 square feet illustrating position of huts (numbered 1-4) and the area utilized by the guinea pigs at the end of first, third, fifth and seventh weeks. The entire field was utilized at the end of the eighth week.

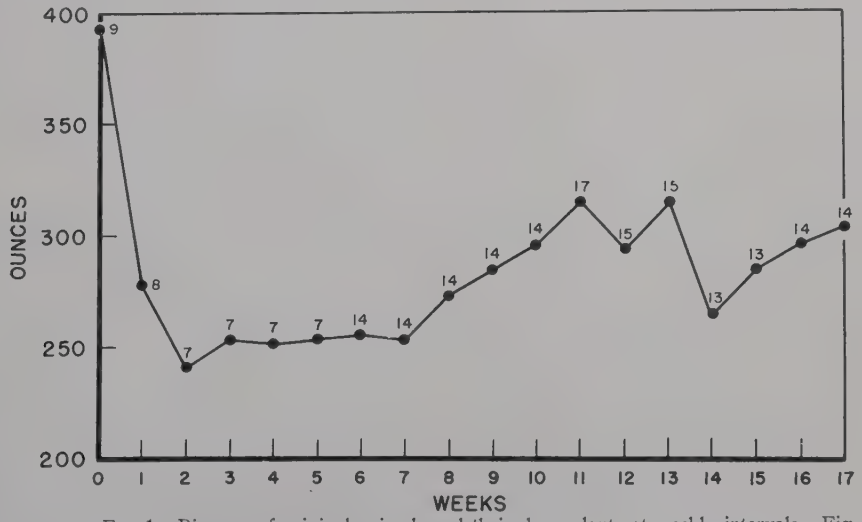

Fig. 1. Biomass of original animals and their descendants at weekly intervals. Figures in graph indicate number of animals.

that the first litter was born alive and the biomass began to increase. It was about the same time (7th week) that the animals began to utilize the entire field (Fig. 2). These data suggest that the animals did not adapt to the new environment until 7 or 8 weeks. Even after the eighth week, the number of animals and the biomass fluctuated considerably, possibly indicating a tenuous adaptation.

TABLE I. Weight, Longevity and Reproduction of Nine Adult Guinea Pigs Originally Placed in Semi-natural Environment

Original Animals	Race	Sex	Original Weight Ounces	Wt. at 1 week Ounces	Total No. Days in Colony	Week Replaced	No. of Litters	No. of Litters from Descendants
A_1.....	Multi-colored	♂	36	31	287	..	..	..
A_2.....	"	♀	49	Dead*	6	4th by A_4	0	0
A_3.....	"	♀	49	34*	9	Not Replaced	0	0
R_1.....	Red	♂	27	25	84	..	..	..
R_2.....	"	♀	47	42	98	..	1	0
R_3.....	"	♀	42	37	126	..	2	3
C_1.....	White	♂	52	46	287	..	..	..
C_2.....	"	♀	38	31	210	..	3	2
C_3.....	"	♀	54	30*	287	..	4	4
Total.	..	..	394	276	..	..	10	9

*Produced stillborn litter.

Runways were made through the grass until they became well beaten trails. Most of the runways were between huts. Only after the tall grass in the unoccupied quadrant was cut did the animals utilize the area and make runways. The runways were made by beating the grass down with their feet, although some weed stems were cut with their teeth.

Food. For food, they depended largely on the green grass of the field. They ate only the distal portions of the grass at first, but as the year went on they began to clip the grass close to the roots. In the winter, weed heads and the dried grass were eaten, but the animals became more and more dependent upon the food supplied to them. When snow was on the ground they ate only oats and carrots.

Periodicity. Guinea pigs were active throughout the year and showed no change in their behavior, except for restriction to the huts during periods of deep snow. No annual cycle of reproduction was observed and young were born at intervals throughout the year.

The daily periodicity of the guinea pig is apparently governed to a considerable extent by temperature and the intensity of the sunlight. During the summer, they are most active when the sun is low on the horizon or has already sunk. They avoid the intense sunshine at midday. On cloudy days, they are active at intervals throughout the day. They do not appear to be active in darkness, for when the colony was visited at night there was no activity outside of the huts. During the winter, the warm midday and colder twilight hours are periods of increased activity. A 15-minute-interval census conducted on January 30 showed most animals out at midday, with a decrease in number in midafternoon, and another increase in number of animals outside at dusk.

Reproduction. For the three adults which mated and reproduced in the colony, the time between births was 68, 69, 71 and 102 days. Apparently all but the last mated immediately after parturition. There were three females which were born and bred in the colony. Two of these had their first litters between 106 and 113 days, indicating that they mated at about 40 days of age. The other had her first litter at 149 days, indicating her first fertile mating occurred at about 81 days of age.

The mating activity of the males is not as well known as that of the females. However, all of the litters born in the colony were sired by two of the original males, judging by color patterns of the offspring. The males born in the colony showed considerable interest in the females and often mounted them when they were not in heat, but they probably did not succeed in achieving any actual copulations.

Of nine litters sired by colony males, five were by the white male, and four were by the multicolored male. The white male bred four times with white females and once with a young red female. The multi-colored male bred only with females born in the colony, two white and two red. The only multicolored female failed to breed after giving birth to her single offspring shortly after she was placed in the colony.

SOCIAL BEHAVIOR

Ingestive. The social relationships in ingestive behavior primarily involve the nursing of the young. During the first four days of life, young guinea pigs depend almost entirely upon milk for nourishment. Sometimes the young guinea pigs will nibble on their bedding of shavings or straw within a few hours after birth, but actual ingestion of solid food does not usually begin until about four days. Once they begin eating solid food the amount of time spent in sucking is considerably reduced. After the young are 15 days old they are rarely observed sucking, although they may occasionally be seen for short periods at the nipples of the mother until they are 28 days old.

Generally the guinea pigs did not compete with each other for food. Often several fed together on a single carrot. Occasionally one individual pushed another away from a handful of green grass, or one pulled a blade of grass away from another individual, but there was no hoarding or storing of food.

Eliminative. The only social relationships connected with eliminative behavior are those of the mother licking the anal region of the young in order to stimulate them to defecate and urinate. While the mother is licking the young the latter relax and permit themselves to be turned over and at the same time they utter a highpitched series of squeals. Occasionally the adults exhibit coprophagy. The feces are dropped anywhere and they usually accumulate in the huts. Consequently all animals are in close association with the eliminative products of their nest-mates.

Contactual. Huddling is the only form of contactual behavior. This is particularly prevalent during cold weather when the animals preserve their body heat by huddling together. At times they line up side by side in long rows beside a hut apparently to keep warm. There is no grooming other than the mother's licking the young for several days after they are born.

Investigative. Social investigation is infrequent and occurs primarily as an expression of sexual interest in the females by the males. Strange individuals are thoroughly examined by most residents, particularly the adult male.

Allelomimetic. Allelomimetic or contagious behavior in guinea pigs is most frequently displayed by their readiness to follow each other. Within the first week, young began to follow their mothers and to a lesser extent other members of the colony about field. The young follow each other and the adults for about a month during which time they gradually become more independent in their movements. Occasionally adults exhibit allelomimetic behavior by following each other, particularly when frightened. Males frequently follow females while trying to smell or mount them. The well-defined runways in the grass are often avenues for a group of animals to move along together.

The periodicity of the guinea pigs tends to make them actively forage at the same time. Frequently they form small groups of four to seven animals while feeding in the field. These groups may occur at particularly favorable feeding sites, or in response to mutual stimulation. The fact that the groups form in different places suggests that the individuals may be responding to each other. The looseness of these groups, however, is indicated by the readiness with which animals leave them and feed alone.

When the animals are in a group they occasionally utter a rapid series of chirp-like sounds. This vocalization apparently serves the function of maintaining group continuity, since it keeps all individuals in the group informed of each other's presence. It may also serve as a greeting when two individuals meet. These chirpings reach their greatest intensity when a female is approached and subdued by a male.

The grouping of the animals in the huts when examined each day showed no particular pattern (Table II) except that some individuals were never found together. Absence of association was particularly true of the multicolored individuals (A_1 & A_4) which were most often found together, but were seldom with other individuals. Apparently the animals went to the huts irrespective of the social contacts made there. The only forms of mutual stimulation in these temporary groupings may have been the result of mother-young and female-male attractions.

Epimeletic. Almost no attentiveness is exhibited among guinea pigs except the care mothers show their young in grooming and nursing them. The ties between the mothers and young are strong (Seward and Seward 1940). The mothers often remained near their young when they were being weighed. At these times the mothers seemed solicitious of the young, running about nervously, while the other animals ran away. Mothers responded to the whistling of the young by going to them. However, this response to the calls of the young was not immediate nor well directed.

Et-epimeletic. The request for attention is well developed in guinea pigs. It first appears among the young, who often whistle when alone, or when deprived of their mothers. Although the young may not whistle when the mother leaves them, they will call for her when hungry, or when the mother comes near them. Mothers often respond to this call, or show some excitement when prevented from coming to their young. As the young grow and begin to wander about by themselves they frequently give the whistle when they find themselves alone in strange places. The presence of other individuals lessens their propensity to call, but if hunger stimulates the call, only their mother can satisfy them by permitting them to nurse.

Animals of all ages give the et-epimeletic whistle in response to the human observer who feeds them. They quickly associate sounds or the sight of the feeder with the receipt of food and respond by whistling whenever he is heard or seen. Even those free in a field came running and whistling

when offered fresh grass. Allen (1904) identified this whistle as a hunger call; however, it may be given at any time as a demand for attention, whether hungry or not.

Sexual. Sexual behavior develops early in guinea pigs. Young males less than 25 days old, while still nursing, sway their hips and rumble as they walk about a female and try to mount her. This courtship pattern of rumbling and hip-swaying is characteristic of males parading before females, but it is not an essential part of the primary sexual act (Young and Grunt 1951). In a larger society this behavior is not expressed as early, probably because the adult males exert some hostility toward young males exhibiting it. When the males are about three months old they show considerable interest in the females, chasing them around and trying to mount them. Attempts at mounting are made towards all females, regardless of the estrus stage, pregnancy, or age.

Adult males showed more selection of mates than juvenile males and tended to remain only with females in estrus. When the females were in estrus, the adult males kept other males away from their mates. Preliminary sexual behavior was observed at all times of the year and throughout the hours of daylight; however, no copulations were seen in the field. For a complete description of sexual behavior see Young and Grunt (1951).

Agonistic. As soon as the three breeds of animals began to associate with each other, severe fights developed among the males which were previously strange to each other. The first fights were between the red and the white males. Since the red male was much smaller, he was subdued by the white male after a series of fights which were evident from the torn ears, cut lips, and scattered fur. Although the fights between these males continued for some time, they gradually diminished in frequency as the red male avoided the approach of the white male, which gave warning by chattering his teeth. Subsequently, contact between the white and multi-colored males was made and most hostilities continued between them. These animals were nearly the same size and the fights were particularly severe. Frequently the lips of the rivals were cut open and parts of the ears were torn off and deep wounds were inflicted on the rump. Despite these injuries, neither male permanently submitted to the other. Instead, they developed a pattern of mock aggression toward each other and entered into bluffing combats without coming into actual contact.

These initial displays of aggression among the males appeared essential for the establishment of territories, each being guarded by a male. No territories developed, however, and the males moved freely among the huts. One male usually dominated the other in the vicinity of his original hut, but this did not keep the others out or prevent the others from entering in the absence of the resident male.

During the combats the males faced each other and chattered their teeth. Then they approached each other with heads up and noses pointed high. From this position they made a series of quick leaps at each other, with their months aiming at the head of the opponent. Usually one such encounter sent them apart and they circled about waiting to make another. Often there was no victor and both drifted apart while feeding.

If one male was beaten he retreated, but was not usually pursued. On occasions when the victor did pursue the vanquished, the latter usually turned around and prepared for another encounter.

After a month of these conflicts, neither of the animals showed any further injuries, although disputes continued between them. The red male had become so subdued that he was not allowed to enter the huts and subsequently died 2½ months after the experiment began. Rivalries developed from time to time between the adults and young males, as well as among the young males themselves. However, none suffered serious injuries. Only a little fur was occasionally seen about their scenes of battle. The adult males tolerated the young males, except when the young animals tried to mate with the females.

TABLE II. The number of days individuals were associated in same hut during a period of 31 days in August, 1952

		A_4	R_1	R_2	R_3	C_1	C_2	C_3
A_1 ♂	..	24	0	2	3	0	3	0
A_4 ♀	..	..	0	0	1	0	0	0
R_1 ♂	..	..	..	10	15	10	5	9
R_2 ♀	..	..	..	..	16	10	14	13
R_3 ♀	..	..	..	..	..	7	8	9
C_1 ♂	..	..	..	..	..	..	11	12
C_2 ♀	..	..	..	..	..	..	..	8

Often bickering could be heard within the houses, but it was apparently not serious enough to drive the members out or to cause injury.

Some antagonism was observed among the females. These disputes were mild and usually took the form of one female keeping another from her particular hut. The females varied considerably in their tolerance of other females, both among individuals and from time to time. Several females seemed to be able to dominate the others on occasions when conflict arose but there was so

little opportunity for conflict that disputes rarely occurred.

Guinea pigs exhibit both escape and freezing behavior when startled. An unexpected movement of the observer caused them to scurry rapidly into their huts. On the other hand, a strange sound, such as rattling keys, or rustling paper, provoked them to give a low-pitched rumble or purr and to freeze in their positions until all was quiet again. They apparently are quite specific in their response to alarming visual or auditory stimuli; running upon seeing and freezing upon hearing a sign of danger.

Discussion

The aim of this discussion will be to describe the social behavior of the genus *Cavia* as it prevails under natural conditions. Such a description is handicapped by the absence of anything but a few scattered field notes on the cavy in its native habitat and by the necessity of relying upon the study of a domesticated form living under semi-natural conditions. The employment of domestic forms in the analysis of basic social patterns of undomesticated animals assumes no radical change in those social patterns. The validity of this assumption has been indicated from studies of the domestic dog which has apparently retained most of the basic social patterns derived from its wolf-like ancestry (Scott 1950). Furthermore, any description of social behavior of a genus runs the danger of ignoring important species differences; but if Gilmore (1952) is correct in assuming that all the described species of *Cavia* are conspecific, this possible source of error is reduced. In spite of these limitations of the available data, it may be possible to present a somewhat valid picture of the social life of wild cavies.

The social organization of wild *Cavia* may be a polygynous group consisting of one adult male with several adult females and their young. The animals in this group utilize the same feeding area, runways, and burrows. They frequently encounter each other while foraging and may feed and rest together.

The failure of the guinea pigs to establish territories in the experimental situation was possibly the result of the relatively small area occupied, which necessitated a certain amount of familiarity and tolerance among them. Under natural circumstances it is likely that territoriality develops because of the sedentary and aggressive behavior of the males. Within the territory the single adult male is particularly active, investigating the other individuals for signs of estrus or for strangers which may invade from time to time. Strange males are met with hostility and are driven from the area by the resident male. Occasionally an aggressive invader is able to defeat and drive the resident male from the territory. Strange females in any stage of estrus or pregnancy would not be excluded by the resident male. However, most females probably remain in the territory where they bear their offspring and subsequently mate with the resident male. Movements of females are also restricted by the care they must give to their young until weaning. After the young are weaned, the females tend to be more aggressive than at other times and may successfully wander into different territories where they must establish themselves among the somewhat hostile females. Resident females are probably more defensive of their particular refuge or burrow than they are of the entire territory.

The young born within a burrow or under a rock pile may wander about inside their shelter until 3 or 4 days of age. Then they come out and begin to follow the adults along the well-made runways. For the most part they probably follow their mothers, but on occasion they may follow other females or even males. Some natural fostering probably occurs. The males are very tolerant of the young, but offer them no care.

As the young females mature they may wander from one territory to another, but most probably remain in the vicinity of their birthplace. At their first estrus, many of them are mated to their fathers.

The maturing males express their sexual interest early, but they are prevented from sexual contact by the adult male. Some young males may be so inhibited sexually by the adult male that they are sexually quiescent and remain passively in the territory of their birth. The more persistent young males are driven from the territory and go off to live by themselves or with other young males until they reach full size, when they try to invade occupied territories.

This description of a wild cavy society can only provide a hypothetical construct which must be tested by studies of the cavy in its native environment. Until such studies are undertaken, we can at least say that the domestic guinea pig can develop a moderately well-integrated society chiefly characterized by allelomimetic, et-epimeletic, sexual and agonistic behavior.

Summary

1. Wild cavies are sedentary, living in small groups usually consisting of one male and several females. When brought into captivity, males may not even tolerate females except at the height of their estrus.

2. The domestic guinea pig living under semi-natural conditions is slow to adapt to its new environment. Once the animals become accustomed to a situation, however, they are able to maintain themselves as a society, though a weakly organized one.

3. Guinea pigs are predominantly crepuscular, avoiding direct sunshine and darkness.

4. Their social behavior under semi-natural conditions is chiefly characterized as follows:

a) Allelomimetic behavior, with the young following the adults and the males following the females.

b) Et-epimeletic behavior, when the young whistle loudly in the absence of adults and the adults whistle for attention supplied by the human caretaker.

c) Sexual behavior, which matures early and is frequently expressed by the males as they follow both estrus and anestrus females.

d) Agonistic behavior among the males which fight vigorously, particularly in the presence of estrus females. Females are less antagonistic but display a weak and flexible social hierarchy.

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THE ANALYSIS OF SOCIALIZATION IN SHEEP AND GOATS

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In recent years, the ecological significance of social behavior in animals has attracted increasing attention. In turn, social behavior has received more analytical investigation. A number of authors have observed that the establishment of normal social relations for the species often seems to depend on normal parent-young interactions at and shortly after birth or hatching (cf. review by Scott, 1956). This process of socialization is frequently difficult to analyze experimentally in sufficient detail and replication in wild animals, partly because they are wild, and studies on related domestic forms will help guide investigations on wild animals.

The purpose of this article is to describe and analyze mother-young interactions in sheep and goats with special reference to the process of socialization. The animals studied, with the exception of some initial observations on parturition in sheep at the University of Wisconsin, belonged to the Cornell Behavior Farm of Cornell University, where the author was a guest during 1952-53 as a research fellow of the National Institute of Mental Health, United States Public Health Service. I am indebted to those in charge of the University of Wisconsin Experimental Sheep Barn and to the staff of the Cornell Behavior Farm for their kind assistance in various ways.

The pattern of mother-young interactions will be illustrated by one example each for a domestic sheep and a domestic goat, for the first few hours after birth, followed by an interpretation of this behavior, with special reference to the establishment of the maternal-filial bond. Finally, some aspects of later social development will be summarized.

Examples of Mother-Young Interaction

The object of describing specific examples of mother-young interaction during and after the birth is to attempt to convey an objective and realistic conception of the complexity of the events that are involved.

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Mother-Young Interactions in Sheep

This parturition was observed at the University of Wisconsin Experimental Sheep Barns, May 8, 1952. Because of limitations of space only the more significant portions of my notes are given in detail. Observations were continued for four hours. This ewe had had lambs for at least three previous years.

6:55 P.M. A translucent, yellow-brown water bag, about four inches in diameter, is protruding from the vaginal opening.

7:00. There is a gush of water from the vagina. The ewe is restless, blows through nostrils, and seems to nibble at ground. Keeps calling *ma-a-a-a-a*. Chews cud a little, and licks her lips.

7:05. Very restless. Once gets on knees and spreads hind legs a little, but rises at once. Water bag now hangs down a little farther.

7:07. Sniffs or blows through nostrils at ground and paws straw with one forefoot. Drops to knees momentarily. Rises, and one minute later lies down and gasps continually, with nose raised. In labor, *i.e.* belly contracts front to back, and ewe makes straining sounds as well as giving loud sniffs or sudden forcing of air out through nostrils.

7:14. Takes first rest. Soon resumes straining.

7:16. Rises to feet—water bag is broken and sticks to udder at lower end. Ewe puts nose to straw. Resumes labor while standing, and then rests.

7:18. Lies down and resumes labor.

7:20. Rests. Breathing rapidly.

7:22. Ewe rises and turns to face observer. Drops nose to straw, then lifts head, licks lips, lies down and resumes fast breathing with intermittent straining.

7:24. Rises again and noses restlessly about, turning in one spot.

7:25. Lies down and breathes heavily, intermittently contracting abdomen front to back—sometimes having a strong spell of contractions and lifting head, nose up.

7:27. Rises and mouths at straw, turns about 360°, lies down, and strains again for a while; then breathes heavily with mouth closed. Rests, then resumes straining.

7:29. Rises, picks up straw or hay in mouth and eats. Again eats hay or straw which disappears down its mouth once again. Circles and lies down and resumes straining. Chews cud a few times and breathes heavily—again strains. Each time it strains the first visible signs of the lamb to be born soon, appear as a slight protrusion from the opening of the vagina, being withdrawn when the ewe rests.

7:32. Rises, gives weak "maaa," turns and lies down again, and again labors. (Note that ewe largely stopped vocalizing since active labor began.)

7:35-8:15. Labor continues in the same restless fashion described above.

8:15. Lamb is born head first and feet down doubled beneath it while ewe is lying down. It starts to wriggle as soon as clear of mother. Ewe calls "maaa," rises, turns and at once eats and licks amniotic membranes off lamb, going over its whole body, and at times calling "maaaa" in a very low and rather gurgling voice. Lamb soon raises head, and also licks its lips, and in wobbly uncertain movements brings its head in contact with mother's head.

8:27. Ewe stops licking lamb for first time, and goes into labor again. Returns to lamb in a minute, licks it, again labors, stops labor and again goes to lamb.

8:30 First sound by lamb, a very weak "aaaaa." Soon repeated, as mother licks it.

8:31. Lamb starts to rise, and falls, again rises on hind legs and front knees, front legs apparently too weak to support it. Voice becomes stronger and mother answers.

8:35. Lamb works way to mother on front knees and on hind feet, nudges her abdomen, and suckles her abdomen and hind leg, coming close to teat, but missing it. Ewe continues to lick lamb, keeps circling it, but does not tread on it. Birth membranes protrude from her vaginal opening and hang to the ground.

8:41. Lamb wags its tail a little as it nudges breast of mother between her legs. Lamb keeps turning toward ewe and as she licks it, the lamb also makes licking movements with mouth.

8:42. Lamb wags tail vigorously as it nudges mother's breast.

8:43. Lamb stands up on all four feet for first time. Ewe keeps circling and so works lamb in and out of right position to nurse. Lamb continues to stand and wags tail sometimes, as ewe licks it, even when not trying to suckle.

8:47. Lamb for first time *walks* on all four feet—wobbly.

8:50. Note that ewe licked lamb almost continuously first 15 minutes with very few breaks, licked lamb most of second 15, and then licked lamb only about half the time during last five minutes. Ewe goes into labor again, picks up and eats a mouthful of straw briefly. Turns back to lamb and licks it.

8:57. Ewe lies down and labors.

8:58. Lamb shakes self for first time, while nudging neck of ewe. Note that ewe has answered every bleat of lamb with her "maaaa."

9:01. Ewe eats mouthful of hay. Lamb comes, puts its head along side of hers and takes hay into mouth, mouths but doesn't actually eat the hay.

9:04. Lamb lies down and rests. Ewe paws hay next to it with opposite forefoot, and then licks lamb again. Lamb raises head and licks lips. Thus far lamb has sucked at breast, leg, abdomen and udder, but hasn't hit teat yet.

9:05. Ewe lies down next to lamb and resumes labor. Lamb bleats and she doesn't answer for a moment, but eats mouthful of hay. Lamb bleats and she at once answers. After a few mouthfuls ewe labors again for about 20 seconds and then rises. Lamb continues to rest, and she goes and licks it.

9:10. Ewe lies down to labor, partly on lamb, and I frighten her off. She lies down on other side of pen and labors again, pants and rests.

9:12. Another lamb is starting to show at birth opening.

9:13. First lamb has been resting since 9:04. It bleats and ewe rises and licks it. She soon lies down and labors again, also calls occasionally.

9:15. Ewe rises, breathes heavily and rests, turns and lies down.

9:17. Second lamb is born—ewe stops and rests when lamb is more than half out. The lamb starts to move—ewe rises, and lamb falls out rest of way. She at once turns, licks and eats the membranes which cover the lamb.

9:20. The second lamb bleats when less than three minutes old (first lamb was calling).

9:23. First lamb finds teat and sucks teat for first time at 1 hour and 8 minutes after birth.

9:25. First lamb sucks briefly at membranes hanging from vagina of mother, and then it briefly licks the other lamb.

9:27. Ewe finished eating membranes off of second lamb.

9:30. Ewe stops licking the second lamb for first time, and looks around to see first lamb who has been sucking on a teat for over one minute.

8:31-10:00. First lamb (male) sucks two more times. Second lamb (female) stands at 9:49, and after pushing against neck and front part of abdomen of ewe many times, manages to find teat and sucks for first time at 10.01. Wagged its tail and ewe smells it under tail for first time. Loses teat after about 15 seconds.

10:04. Second lamb lies down to rest. Ewe has just about stopped licking it.

10:05. After-birth starts coming out.

10:07. Ewe starts eating afterbirth. Soon stops and apparently eats hay instead.

10:12-10:19. Ewe finishes eating the afterbirth. The two lambs are lying down together.

10:24. Second lamb apparently finds teat again and sucks; found teat when ewe stepped forward and turned slightly toward lamb which was nudging her in the fore part of abdomen. It soon loses teat. First lamb continues to lie down and rests, apparently asleep (immobile) for the first time.

Mother-Young Interactions in Goat

This parturition was observed at the Cornell University Behavior Farm, November 22, 1952. Female 7-49. Has had young before. For two days, Female 7-49 has stayed in barn, and has not gone out with the herd.

11:40 A.M. For one hour 7-49 has been lying down in hay in depression she made, and does not rise when I touch her. Does not chew her cud. Now starts rising restlessly at occasional intervals, turning about and at once lying down again. Also starts to strain with head and neck tensed and extended, chin almost in line with throat, ears laid stiffly back and mouth closed. Coincidentally there are movements of lower abdomen forcing backward, and tail is partly raised. Apparently female is in early labor. While standing she hunches her back up (vaguely suggestive of post-copulatory position).

11:45. She gives typical call of mother to kid, *i.e.* short, light, low-pitched series of notes with 3 to 5 notes in a group, and she looked back while calling. These vocalizations were uttered long before kid was born. She then lies down.

11:50. Female 7-49 starts to grunt occasionally, and a string of mucoid substance begins to protrude from the vaginal opening. The area beneath her tail trembles. Tail rises slowly above the horizontal, as she chews hay briefly from hay crib under her nose. Again tail rises slowly above the horizontal and region about birth opening trembles. Then she lies down again, and starts giving low, short bleats in series, with each series timed to her labor; this coincidence is repeated several times. The movements of labor begin with a straining grunt or groan given with the head forward. The female gets on her knees with tail raised high—then lies down again.

11:55. Mucoid substance from birth opening now extends downward to distance of about a foot. The goat rises, eats hay briefly, and again lies down. She starts to breathe rapidly with mouth closed. Actually eats hay, and later chews cud very briefly.

12:20 P.M. The external margins of the vagina gape whenever the female strains, and this straining is now commonly accompanied by low bleating. At same time the whole surrounding area of bare pink skin bulges outward as if kid is near mouth of birth canal.

12:32. Amniotic sac bulges out and breaks, and part of the kid protrudes outward. Female looks back, chin raised, and bleats repeatedly—then she yawns widely.

12:34. The kid is forced out at 12:34. The birth is apparently painful and the mother screams loudly several times, starting forward as the kid is born. The female then licks her own external genitalia, meanwhile bleating repeatedly in low, short notes. In the meantime, the kid snorts lightly, struggles to a sitting position, and then starts bleating in a very weak voice, like a tiny trumpet. Soon the kid begins to call more loudly, and the mother turns to it, touches it gently with her nose, yawns, and as the kid continues to bleat more loudly, she again touches it with her nose, and again yawns.

12:42. The mother then starts licking the kid, and the kid bleats less often and more lightly. The mother apparently eats the amniotic membranes as she licks them off the kid. She stops to yawn. The kid starts to struggle up on its hind legs, but soon slumps down again.

12:44. The mother stops licking kid to yawn again, and then lies down. A second kid is now born, coming out head first with front and rear legs extended and twitching. The mother apparently strained only once for this second birth. The kid immediately after birth starts snorting or sniffing, shakes its head from the damp membranes that cover and cling to it, and then lifts its head and rights itself within 20 seconds of birth. The mother at once starts to lick and eat the birth membranes commencing from the thigh region of the kid and proceeding forward. The second kid does not bleat immediately after its birth, unlike the first kid.

12:45. The first (older) kid stands up on all four feet for the first time; it is very wobbly and after about 10 seconds flops down again. It continually utters light and relatively low, single bleats, while the mother licks off the second (younger) kid.

12:49. The first kid walks for the first time, taking a few steps forward. It remains on all four feet for some time, although wobbling.

12:50. The mother bleats or grunts (low, short notes) for the first time since the birth of the first kid, and she leaves off licking the second kid to sniff at the rear end of the first kid. She then shakes herself for the first time since observations began this morning, and resumes her licking of the second kid. The first kid starts bleating again, and the mother licks at its rear end.

12:52. The mother yawns.

12:54. The second kid begins to suck hair on mother's leg, and it bleats briefly for the first time as it moves back toward teat. Meanwhile the first kid has wandered off some six feet and keeps on uttering a series of low bleats.

12:57. The second kid seizes and then loses the tip of a teat, but keeps trying and soon regains it. Its head wobbles so that it again loses the teat. Meanwhile the first kid starts sucking and pushing with its muzzle at the wooden wall of the barn, and wags its tail meanwhile. The second kid has just worked its way past the rear end of the mother.

1:00. The mother leaves the second kid to go and lick the first kid which was five feet away from her, and then the second kid starts to bleat. The first kid also bleats as she licks it. It has been on all four feet all this time. The first kid moves between the mother's front legs and stops bleating, and sucks at hair on her hind legs and abdomen, between the teats, at the udder and at the sides of teats which it nudges for the first time. It soon gets the tip of the swollen teat in its mouth and at once loses it.

1:05. The second kid is still bleating, while the first kid is silent with the mother still licking it.

1:07. The first kid grabs and holds a teat for the first time, wagging its tail while mother licks its rump. The mother occasionally grunts or utters low bleats consisting of one to three notes, especially when the second kid bleats after struggling to get close to her again, coming from a distance of five feet. The second kid starts sucking at hair on rear of udder, at hair on mother's legs, and then at side of teat; it also nudges her udder from the rear.

1:12. The first kid manages to seize a teat again, and then loses it, and sucks hair on the breast of the second kid. The second kid drops to its knees and sucks at the region of the udder of the first kid. The first kid moves off and sucks hair of mother between front legs. Note that both kids tend to work beneath the mother, who keeps on licking the first kid.

1:15. The kids keep trying repeatedly and persistently to suck, and often they seem to keep working toward udder. The first kid wags tail slightly when mother licks it, even when not trying to suck. Note that mother pays no attention to remnants of amniotic membranes that have slipped off kids to floor of barn, but only eats those remnants still on kids.

1:16. The first kid again gets a teat, and loses it in about 10 seconds. The mother started licking the second kid again, and it soon starts sucking at hair on her abdomen. It works its way back to region of udder, nudges the udder, and gets teat but the teat slips repeatedly out of its mouth.

1:20. The second kid manages to hold teat for about 5 seconds. The mother licks it on rear, and it keeps wagging its tail all the while.

1:22. The second kid gets and holds teat 7 seconds before losing it, then manages to hold it again for 7 seconds, and at 1:25 for about 15 seconds, and again at 1:27 for about 15 seconds, before losing it. Soon it is back on the teat again.

1:25. Mother yawns, and again at 1:28. Note that this female has done relatively little turning and shifting, and the kids seem to find the teats largely by their own efforts.

1:30. The first kid seizes a teat and sucks.

1:32. I lift up the first kid (still very damp), and move it about 8 feet from mother, and for the first time it gives loud, high, long (2 seconds) piercing screams of distress. I put it down, and the female goes part way to it and it goes rest of way to her and is nursed. She gave low grunts (in series of 1 to 4 grunts each) in response to its bleating (*eh-eh-eh-etc.*) as it moved toward her. The second kid also went to her right after she grunted ("bleated").

1:35. The mother again yawns. A bag of fluid, some 4 inches long, still dangles from her vagina as for some time now, and the afterbirth has not yet been passed. She has been licking the kids off and on ever since they were born, and they have been trying to suck ever since they could stand. Both of the kids have been on their feet most of the time since first they stood, walking about and under the mother in a rather wobbly way.

1:45. Observer leaves.

Establishment of the Bond between Mother and Young

In general, the pattern of behavior at parturition appeared to be basically similar in sheep and goats, although minor differences existed. A total of four cases including the instant of birth were observed in sheep and eleven in goats, while 7 additional cases in sheep and 19 in goats were observed within an estimated hour or less (often much less) after the birth had occurred. The observations on sheep agree with Scott's (1945) more general description of the development of behavior in sheep.

Most of these births were watched from a distance of a few feet, and with few exceptions the animals, most of which were very tame, seemed undisturbed by the presence of a human observer. Behavior of the mother and young in the hours subsequent to the birth was often watched through one-way glass in a laboratory room in which mother and young were placed.

In the 41 cases of mother-young interaction that were observed immediately or shortly after birth, individual variations in behavior of both mother and young were often observed. Repeated observation frequently combined with experiment helped to bring out the significant elements and to clarify the interpretation of mother-young interactions.

Some of the more significant phenomena determining the manner in which the social bond is established between mother and infant are suggested in the following sections, which deal in a step-wise fashion with the establishment of the bond between mother and young, starting from the instant of birth.

1. *Initial Responses at Birth*

In both sheep and goats parturition might take place with the mother lying down, or standing. In the case of only one female goat (described above) was the birth apparently very painful and accompanied by a loud scream of distress. As a rule the first response of the mother ewe or goat following the birth was to turn at once and begin licking the membranes from the newborn; occasionally the mother might lick her own external genitalia briefly before tending to her young one. Frequently, the mother would give a low-pitched, relatively short bleat (goat) or gurgle (sheep), which is the typical parturient voice, as she turned to face her newborn, but occasionally she might not begin this call for one-half hour or more. Sometimes a pregnant animal would give this call shortly before parturition.

A kid when born as a rule came out smoothly and head first; in one case (one of triplets) a kid was seen to come out feet first. Quite often the kid showed no movement until it was completely out of the birth canal and on the floor or ground. But one kid lifted and shook its head when partly out, another gasped as soon as its head was clear of the vagina, and in a third case, the kid's head was out for 10 to 20 seconds before the body was born and the kid bleated at this stage of the procedure. A kid or lamb on being born might bleat at once as might be expected since it is wet and roughly enters a colder environment than the one it has just left. But some kids or lambs did not call for some time after their birth.

In one case the head of a kid came out while the mother goat was lying down; she then arose, withdrew the head of the kid back into her body, turned and licked at the gelatinous fluid that had spilled out from beneath the kid, and all the while she continued bleating. The kid was born shortly afterwards.

It may be seen that the initial events at birth are quite variable in different cases. The most consistent and perhaps most significant event would appear to be the turning of the mother to face the newborn, associated with the fresh birth odor.

2. *Licking and Eating of the Birth Membranes*

What are the stimuli that cause the mother to lick and eat the birth membranes and fluid from the newborn? It is probable that some specific odor is one important stimulus. A ewe and a goat were seen to turn and lick a puddle of gelatinous fluid that had emanated from the vagina shortly before parturition started. A ewe was easily led from the pasture into the laboratory by holding a few inches from her nose her newborn lamb, which was not vocalizing nor moving very often, and with which the mother had not yet been permitted any contact. It was possible to attract this ewe for short distances by a rag rubbed in the fresh birth membranes, but not with a rag soaked in water.

The thirst of the mother may be a minor factor facilitating licking of the birth membranes. Ewes, particularly, are likely to drink much water during the first few hours after parturition. Once the kid or lamb is dry the mother licks it very little. One kid shortly after it had dried off, was made thoroughly wet again with water, but was not licked again by its mother, except for a few desultory licks normal for its age.

Specific hunger perhaps is a factor in licking and eating of the birth membranes, and might perhaps increase the sensitivity to special odors. Pregnancy involves considerable drain on the energy resources of the mother, and eating of the fetal membranes and placenta may help restore some essential nutrients to the mother. Usually the amniotic membranes were eaten, while the placenta often was not eaten. The degree of licking of the fetal membranes varies greatly in different females. One mother goat scarcely licked her two kids at all, but nevertheless accepted them.

3. *Vocalizations*

The young are stimulated to bleat on hearing the mother call, or on seeing her moving at a little distance away. The mother as a rule promptly replies to the bleating of her young with a characteristic series of low-pitched and short bleats in the goat, or with a low-pitched gurgling call in the ewe, and the mother at the same time goes to the young one. After it has been licked for a while by the mother, the young one is more likely to bleat whenever the mother for any reason leaves it to go more than a few feet away. Similarly, the mother which has had a chance to become conditioned to her young, is more likely to bleat or give distress calls when the young are taken from her. The distress call in both adult and young of sheep and goats is a relatively prolonged, loud and high-pitched scream or moan, and is given, for example, under stress of human handling as well as under a number of other conditions apparently indicative of distress (pain, hunger, etc.).

A lamb or kid isolated immediately at birth is likely to vocalize but little. One such lamb became attached to the human observer, would reply to his crude imitation of the maternal voice, and would also bleat promptly when he reappeared after a brief period of absence, even in the absence of vocal stimulation.

The initial importance of vocalizations in bringing mother and young together is correlated with a low threshold of maternal responsiveness to bleating of the young when compared with other aspects of maternal behavior. Thus, a mother sheep or goat often replies vocally to the bleating of any young one of its species, but she may then rebuff the approach of the young one by butting it away. A goat mother may even bleat in response to the distress cries of a lamb, or a ewe to those of a kid, but neither mother on smelling the young one of the other species will have anything further to do with it. One signal stimulating and permitting the kid or lamb to nurse is the abrupt cessation of movement by the mother who then stands still while the young one sucks. This maternal response has a definitely higher threshold of stimulation than does the maternal response to vocalizations of the young. Often a mother goat or sheep may answer and call her young one to her, but then withdraw from its attempts to suck.

4. *Maternal Defense of the Young*

Most of the observations on maternal defense were of goats. The mother goat defends her newborn against the approach of other goats, regardless of sex or age. This defense serves to prevent disturbance of the normal interaction between a mother and her newborn kid which is necessary for the establishment of a firm bond between the mother and kid. Older kids not infrequently try to suck mothers not their own, and if permitted this would often prevent smaller and weaker kids from being nursed by their proper mothers. A mother of low dominance may be driven from the vicinity of her kid by larger, stronger goats, as was seen in several cases. The newborn kid may then soon become lost in a crowd of goats, and being very indiscriminating in its attempts to suck, tries to suck strange females, males and older kids of either sex, alike. It is promptly butted away in most instances, receiving particularly bad treatment from the older male kids. This adverse treatment very probably serves to condition the kid against older goats, making difficult subsequently the establishment of a normal bond to its own mother.

An experienced mother with newborn kids generally defends them effectively, and may even attempt to drive from the vicinity of the kids, males much larger and stronger than herself. The normal adult males treat this aggression tolerantly and soon move off, but castrate males may react intolerantly by fighting and may even drive the mother temporarily from her young ones.

5. *The Young Stand Up*

Before the young one ever attempts to suck it usually struggles to its feet and stands up. The kid or lamb first succeeds in standing anywhere from 10 minutes to one-half hour or more after birth. Licking by the parent may stimulate its efforts to rise, but is not essential, since lambs or kids isolated at birth manage to stand and walk. Usually the lamb or kid sprawls flat shortly after first rising to its feet, but soon persists in struggling up again, and maintains balance longer with every effort. It is not long before it can easily stand for many minutes instead of seconds.

6. *Initial Sucking Attempts by the Young*

Its tendency to go toward a large moving object helps bring the young one in contact with the mother. Kids or lambs that had recently stood up for the first time and have not yet been nursed could often be induced to move directly away from the mother and to follow after a human observer who merely placed himself near the young one and then walked slowly away from it.

The inexperienced lamb or kid will first attempt to suck whatever object, animate or inanimate, or whatever part of the body of the mother, with which it happens to come in contact at the approximate level of its own height. It will particularly suck on protuberances, normally first at the hair on the mother's body. The tendency of the kid or lamb to work between the legs and beneath the body of the mother, combined with its persistence, eventually brings it near the udder and teats. Once having seized and held a teat the young one shows a greatly increased tendency to return directly to the teat on losing it, and soon succeeds in sucking regularly and effectively on the teat.

The mother ewe or goat sometimes appears to assist the attempts of her young to be nursed, by moving her hind quarters into position, and sometimes even lifting one hind leg on the same side as the young one. As an opposite tendency she frequently breaks off the nursing in order to lick the young one from some new position.

7. *Interactions during Nursing*

As soon as the young one is nursed it frequently but not always wags its tail, and the mother as a rule promptly smells beneath its tail. One's impression is that this is a relatively stable position. Presumably the wagging of the tail helps waft any scent that may be present. Tail wagging by the

lamb or kid may be stimulated not only by sucking, but also by contact of the mother's nose with the region at the base of the tail, and at times tail wagging is associated with bleating, independently of contact or of sucking.

It seems not unlikely that one reason that a goat has a beard is to facilitate the reciprocal contact stimulation involved when a mother brings her nose near the rump and tail of her kid.

8. *Hiding of the Young after Initial Nursings*

After the newborn lamb or kid has been nursed more or less to satiation, it shows reduced responsiveness to the mother, lies down and sleeps. The mother may then leave it to go off and graze in the general vicinity, sometimes joining the herd when the latter happens to be nearby. Unlike goats, mother sheep rarely stray very far from the lambs, nor do lambs exhibit the marked immobility often displayed by very young kids on approach of a person (J. P. Scott, personal communication).

An example will be given. A kid born out in the pasture was led when dry by its mother into the nearby sheep shed, where she left it for almost four hours, and where it remained during her absence lying down in exactly the same spot and in much the same position with head and throat flat on the straw. When the head was lifted and then released by the human observer it was allowed to flop down again, and when the head of the kid was placed to one side it was retained in this new position. The kid made no effort to rise and run away.

For two and one-half days this kid kept the same hiding place, being left alone by the mother for three hours on the morning of the second day. During the forenoon of the third day she came and led it away on the first long excursion of its life. She approached its hiding place in a very alert way—stopping every 20 or 30 feet to sniff the breeze, neck erect and ears pricked forward. I had to hide myself before she would come in to her kid. When she got within 30 feet of the shed she began to bleat, but her kid did not answer until she was visible to it through the entrance to the shed. It then bleated, rose, went to her, stretched its legs and shook itself. As soon as the mother saw her kid she changed the quality of her bleating to a lower, less "worried" pitch, went to it, smelled it, led it outdoors and nursed it. She then led it away, bleating when it fell behind, stopping briefly to permit it to catch up and sometimes to nurse, and soon she had the kid moving steadily behind her in the direction of the herd..

The Problem of Maternal Rejection

If a young lamb or kid be removed from the mother at or very shortly after its birth, and is kept away from her for two hours or more, she is likely to reject it on return to her. This rejection is evidenced by persistent withdrawal from the nursing attempts of the lamb or or kid and by the mother's actively butting it away when it comes near her. Maternal rejection under these conditions demonstrates that the first few hours after parturition are critical to the development of the social bond between mother and young in sheep and goats. The supporting data for this conclusion are presented in Table I. An abstract of these results has been published previously (Collias 1953). J. P. Scott recently informed me that sheep owners often have trouble with maternal rejection of the lamb, particularly where the lambs are taken away and warmed after they are born.

Table I. Maternal acceptance or rejection of young removed from the mother at birth, for various periods of separation from her.

	Length of separation	Number of young tested		Twin controls	
		Accepted	Rejected	Accepted	Rejected
Goats:	15 minutes	4	0	4	0
	2 hours	1	1	1	0
	3-3½ hours	0	2	..	..
Sheep:	40-45 minutes	2	0	2	0
	4½ hours	0	2	1	0

To summarize my experimental results: In 5 of 6 cases where the newborn was separated from the mother for 2 to 4½ hours before being returned to her, the young one was rejected, at least during the first hour after it was restored to the mother. In two of these cases, one of a goat and one of a sheep, the young one eventually died as a result of maternal rejection. The one exception was a kid that had been separated from an experienced mother goat for only 2 hours. It had been removed at the instant of birth without permitting the mother to lick or touch it in any way. It had no twin. It was accepted at once on return to the mother.

In all six cases where the newborn was separated from the mother for only 15 to 45 minutes, it was accepted at once on return to the mother.

There were 8 twins left with their mothers as controls for the separated twin. All the controls were at once accepted and were never butted by the mother.

There were also three cases, not included in Table I, of young not removed from the mother until one to two hours after birth. One of these, a kid, was restored to its mother after 2 hours of separation and was at once accepted. The other

two cases were of lambs, one of which was returned to the mother after 3½ hours' separation and was at once accepted. The other lamb, separated for 1½ hours, was rejected for the first half hour and thereafter was accepted by its mother.

Although there are only five cases presented here of experimental maternal rejection of young temporarily removed at birth, these data are strengthened by the fact that only in these 5 instances out of 41 kids or lambs that were observed within one hour after birth was the young one ever seen to be butted by its own mother on the day of birth.

In these experiments, with one exception, it was always the young one and not the mother which was removed in separations. During the period of separation the young one was generally kept alone in a laboratory room. All of the mothers referred to in Table I had previously experienced parturition.[2]

A specific example of these separation experiments leading to maternal rejection will be cited. On April 8, 1953, a ewe (Female 23) had twin lambs, male and female, and the latter was removed at the instant of birth. Four and one-half hours later this female lamb, which in the interim had been kept alone in a laboratory room, was returned to the mother. At once the mother advanced gurgling, smelled and licked the female lamb and permitted it to make nursing attempts at various places on her body. The lamb persisted vigorously in these attempts and occasionally got the teat but soon lost it each time. Forty minutes later the mother as if becoming irritated at the unusually persistent attempts of the female lamb to suck, butted it from its feet as it came near her head. She then licked it and again butted it as it kept moving toward her, then butted it 15 more times, licking it a little and gurgling occasionally between butts. Every time it rose to its feet she butted it down flat. Her butts became harder and harder, slamming the female lamb off its feet to the floor. Occasionally she still licked this lamb, although she butted it 17 more times as it persisted in trying to nurse. She now withdrew promptly whenever the female lamb got anywhere near her teat or touched her udder, and kicked one hind leg up at these attempts, especially when made from the rear. After 14 minutes of this aggressiveness toward her female twin, the mother lay down, but when the female lamb came near her, she pushed it violently away with her snout 5 times, hissing or blowing each time that she did so.

Meanwhile, the male twin, who had been lying down rose to his feet, and shortly after the mother also got to her feet and butted away the female twin, and then permitted the male lamb to nurse for about 20 seconds, smelling and tolerating him. Then he lost the teat, and the female lamb seized and held a teat for 5 to 10 seconds; the mother smelled under the tail of this female lamb, and at once moved off. Again, the female twin tried to nurse and the mother withdrew so sharply that this lamb was caught by the movements of the ewe's legs and thrown head over heels. The female lamb persisted in its attempts to nurse, and the mother again commenced to butt it away.

Next day, the mother was locked in a stanchion to enable her female twin to get something to eat, and in subsequent days she gradually accepted and nursed it.

It remains to discuss the possible mechanisms in the maternal rejection of a lamb or kid which has been separated from its mother during the critical first few hours after its birth.

It was considered that partial drying of the fetal membranes and decline of the fresh birth odor might be important in causing the rejection. Gibson (1951) observed that a one-day old kid when rubbed with the afterbirth of a female not its mother, was immediately accepted by this female, which had previously rejected it. Mrs. Gibson also found that a newborn kid when cleaned and washed off with a strong detergent was nevertheless accepted by its mother. I confirmed this latter observation on a kid, and got similar results with a newborn lamb. Although it is possible that traces of the birth odor persisted in spite of the thorough washing, the fact remains that a mother may accept her young one after all visible traces of the fetal membranes have been artificially removed. Furthermore, I have successfully transferred a kid, 40 to 50 minutes old, from its mother to another (primiparous) mother, whose own kid was removed promptly at the instant of birth and at once exchanged for that of the older and experienced mother. Both adoptions were permanent in this cross-transfer, although the older kid had been completely licked off by its own mother before the transfer.

In another case a 2 day old kid was rubbed with the placenta of another mother whose own kids had been born about one hour before. She licked, tolerated and nursed the strange kid, but by the following morning was found to have rejected it, *i.e.* she then withdrew repeatedly from its attempts to nurse and often butted it away.

[2] Recently, Blauvelt has reported some experiments suggesting that maternal rejection may be more readily induced in primiparous mother goats (Cf. Josiah Macy, Jr. Foundation, Trans. 1st Confer. Group Processes, 1955).

It was concluded that the birth membranes facilitate but are not essential to the formation of the maternal-filial bond.

The physiological state of the mother at parturition is important to acceptance of the newborn. She is prepared to respond appropriately to the young even before they are born, and may lick puddles of birth fluid emitted shortly before parturition. A female goat, about one-half hour before her kids were born, responded to the distress cries of two strange kids with the typical call of the parturient female, and moved toward them. This call in both sheep and goats is relatively low-pitched, segmented and repetitive. Within a few hours after parturition it is given much less frequently, and gradually becomes higher in pitch. This change in voice of the mother suggests that her physiological state at parturition may be optimal for acceptance of the newborn.

This responsiveness apparently soon declines as suggested in Table I. Additional support for this conclusion is derived from 2 mother goats, who only 2 and 3 hours after themselves giving birth, would not lick nor stay with other kids presented to them (untouched by human hands in one case) immediately after birth of the kids.

The mother is less likely to terminate nursing on the first day than is a newborn lamb or kid, but after a week or two, it is generally the mother who terminates the nursing.

However, since mother goats or sheep may be experimentally induced to reject one but not the other young one in a pair of twins (Table I), it is evident that deficiency in maternal drive cannot have been the basic cause of maternal rejection in most of the cases here described. The mother, as it were, becomes fixated on one twin in the absence of the other.

From this it follows that a very rapid learning process is involved in the establishment of the social bond between a mother and her young. In one instance, three different female goats happened to have their kids within one to two hours of each other. During this period it was found possible to cross-transfer kids from one to another of these mothers and to have them tolerated and nursed, particularly if the kids from different mothers were of the same color. But when retested after several days these same kids were rejected by the same foster mothers, that previously had accepted them. In the interim these mothers and their kids had all been kept together in the same barn, as usual.

Odor and sound as well as color cues are probably used by females in learning their individual young. The frequency with which a mother goat smells a strange young one and the length of time engaged in smelling it are greatly increased when the strange kid closely resembles her own kid in size, color and general appearance.

Vocal cues to individual recognition were not thoroughly investigated. Often mothers and their kids or lambs were seen to reply to each other's bleating from behind partitions or walls as if able to recognize each other's voice. But when a kid, one or two days old, was held behind a partition separating it from its own and another mother, the distress screams of the kid were often answered by both mothers, neither of which could see the kid.

In the first few hours immediately following parturition it seems evident upon close observation that mother and young are becoming conditioned to one another during this very active period. Frequently the kid or lamb manages to seize the teat, and frequently it soon loses the teat because the mother moves in order to lick the young one from some new vantage point, or because of the wobbling, uncertain control that the young one has over its own movements at this stage. This make and break of sucking contacts would seem almost inevitably to lead to a rapid strengthening and specification of the developing bond between the mother and young. In effect the young one is subjected to a rapidly repeated series of learning trials serving to condition it to all sorts of significant and satisfying stimuli—tactile, olfactory, auditory, visual—that rain upon it during one of the most highly sensitive periods of its life. The same conclusion would seem to hold in almost every detail with respect to the reciprocal conditioning of the mother ewe or goat to her young.

Later Social Development

Independent feeding activity of the lamb or kid is associated with increasing indifference of the mother to her young as they grow older. Frequently lambs mouthed hay on the day of birth, but apparently did not chew or swallow it. As the lamb or kid learned to graze it was likely to forage farther and farther from the mother. However, in the event of some disturbance, the young one ran back to its mother.

The frequency of nursing decreases as lambs and kids get older, although a kid or lamb may be nursed occasionally for several months. During the weaning period lambs or kids could sometimes be seen to try and block the mother as she walked along by repeatedly crossing in front of her. If she stopped they would at once try to nurse. The greatest age at which a lamb was seen to be nursed was 4½ months. It is rare to see a kid nursed when more than six months old. However, one kid was nursed at 187 days of age, and right afterwards its mother went to another kid to which she

had given birth 3½ days before and she nursed this kid for about two minutes. In only this one case was a mother goat ever seen to nurse her young from two different pregnancies, on the same day. As a rule the mother goats and sheep apparently discontinued nursing older young well before giving birth again.

Aggressive behavior in its early stages developed as play-fighting in which butting the heads together was generally brief, relatively harmless and did not lead to any definite decision on dominance relations. "King of the hill" was a common game among kids. Kids under daily observation were first seen to butt other kids on the ninth day after birth. The young goats gradually developed consistent dominance relations with each other and with the rest of the herd. This dominance order, when finally established, was definite and very consistent with regard to any given pair of individuals. Within each sex, goats with horns regularly dominated goats without horns, so that the presence or absence of horns helped determine the place assumed by a young goat in the dominance order. All the kids were born without horns except as nubbins, and when present the horns begin to grow almost at once, although slowly.

The dominance order in adult ewes is much more indefinite and more of a give and take nature than in female goats, although placing ewes under stress of hunger and competition for a localized and restricted food supply often brought out consistent, unilateral dominance relations between certain individuals.

The development of sexual behavior was studied mainly among goats. The development of male behavior will be discussed first. Mounting of other kids, male or female, was first seen on the ninth day after birth. This was followed and accompanied by the appearance of pelvic thrusts (12th day) and erections (3 months). Kicking of one leg stiffly forward was first noted on the 12th day. The male call of sexual excitement, a segmented, rolling, low-pitched call, was one of the last elements to appear in male sex behavior. Normal adult males are more discriminating in their sexual behavior than are male kids, and unlike the latter, do not ordinarily mount other males, or mount from the front or side as the male kids sometimes do.

Infantile modes of response persisted for some time after male sex behavior had developed to the point where erection was possible. For example, a 3-month-old male kid followed and mounted an estrous female, but the instant she stopped moving —a signal to the adult male to mount, but to a kid to nurse—this kid dropped down and began to nurse the female. Possibly some frustration was involved in this switch of behavior response. Estrous female goats generally avoid the sex advances of the male kids, may butt them away, or go directly to an adult, full-grown male, who invariably chases the sexually active male kids away from the female. The earliest age of a male goat seen to copulate successfully with an estrous female was from 5 to 6 months.

The sexual behavior of the adult male seems to develop partly from a common basis with certain elements of maternal behavior. His call of sexual excitement is much like the attraction call of the parturient female to her newborn. The smelling and licking of the external genitalia of the female resemble the smelling and licking under the tail of a young kid by its mother. The moving contact of the mouth, nose and beard of the male over the posterior portions of the body of the estrous female also bears some similarity to maternal behavior.

Sexual behavior in male goats is also closely related to aggressive behavior, and the two types of behavior develop coincidently. Male kids, five to six months old, sometimes develop penile erections during prolonged fights with one another.

The sexual behavior of female goats in its development seems to make some use of pre-existing infantile responses, and indeed most kids become mothers long before they have attained their full body growth; they may have a small kid of their own by the approximate age of 11 months. Like a kid when its mother smells under its tail, the estrous female wags her tail whenever the male touches her external genitalia or runs his chin and beard along the side of the rump and flank of the female. Presumably the wagging of the tail serves to waft some special odor about.

The earliest age of a female goat seen to copulate was 5 to 6 months. The copulation was not forced, and this particular female, although not yet half-grown, appeared to be in estrus as judged by the pink and swollen external genitalia, by the persistent interest of the males, and by the way in which the female would stand when mounted instead of moving away. Less than 5 minutes after copulating with an adult male who was at least several times her size, this female kid went to her mother and was nursed. Less than five minutes after being nursed, she copulated with another adult male.

The masculine sex behavior pattern develops in females to some extent, but is seen rather uncommonly and under special circumstances. A female goat, victor in a fight, may pursue the losing female, give a male-like sex call (which in such a

female sounds almost exactly like the parturition call), dart the tongue in and out, swing one leg stiffly forward while running the chin along side of the other female and may even mount. Such behavior is not peculiar to adult females, but develops early. A young female kid, coming into her first estrus at 5 to 6 months of age, was seen to show all of these elements of the masculine sex behavior pattern towards another estrous female kid of approximately the same age as herself.

The association between a mother goat and her female kids often persists long after the kids have become sexually mature adults and mothers. In the case of domestic sheep, Scott (1945) has observed that leadership of the flock may trace to the continued association of related ewes in overlapping generations.

Comparisons between Species

The number of similarities in the social behavior of sheep and goats is striking and is evident on almost every page of this report. The species differences in mother-young interactions are largely quantitative, and would require large series of data to bring out adequately. Species differences in behavior between adult goats and adult sheep are more pronounced. There is much less aggressive behavior within a flock of ewes than between female goats, correlated with somewhat closer flocking of the sheep. The manner of fighting differs in the two species; goats often rear up on their hind legs and then drop down smashing their horns together, while domestic sheep back up and then charge forward, butting their heads together. This difference in mode of fighting is paralleled by a related difference in manner of feeding. Both species graze, but in addition goats often rear up to browse, placing the forefeet against the trunk of a tree.

Detailed comparisons of sheep and goats with wild species of ungulates would necessitate another report (Scott 1945). The possible survival value of normal maternal-filial relations is suggested by the observation made in a winter concentration of white-tailed deer, that fawns (of the preceding year) without mothers were much less wary than fawns with mothers (Kabat, Collias and Guettinger 1953).

Summary

1. Examples are described of mother-young interaction at birth and during the first few hours after parturition in sheep and goats. The reciprocal and regulatory nature of this interaction as a basis for the establishment of the social bond between mother and young is developed.

2. If a lamb or kid is removed from the mother at or very shortly after its birth, and is kept away from her for a few hours, she is likely to reject it when it is returned to her. This rejection is evidenced by persistent withdrawal from the nursing attempts of the lamb or kid, and by actively butting it away when it approaches her.

3. Experimental evidence is presented that the probable reasons for the critical importance of the first few hours post-partum in the establishment of the social bond between mother and young in sheep and goats are: (1) facilitation by attraction of the mother to the fetal membranes and birth fluids as well as to the young one itself, (2) maternal drive is apparently highest at or near the time of parturition, and (3) a very rapid learning process results in early fixation of the female on her particular young.

4. Some aspects of later social development are described: (1) As a lamb or kid learns to graze it is likely to forage farther and farther from the mother, and the frequency of nursing decreases. (2) Aggressive behavior, starting as play-fighting among kids and lambs, develops into a consistent dominance order among the goats, while dominance relations are more of a give and take nature among adult ewes, although placing ewes on short rations often brings out consistent, unilateral dominance relations between certain individuals. (3) The development of sexual behavior was studied mainly in goats. Both male and female goats show the complete pattern of sexual behavior long before they have attained their full body growth. Male kids may mount from the front or side, and often mount other males as well as females, unlike adult males. The sexual behavior of male goats seems to develop partly from a common basis with certain elements of maternal behavior, and is also closely related to aggressive behavior. The sexual behavior of female goats in its development seems to make some use of pre-existing infantile responses. The masculine sex behavior pattern also develops in female goats to some extent. (4) The companionship between a mother goat and her female kids often persists long after the kids have become sexually mature adults and mothers.

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SOCIAL ORGANIZATION IN RED JUNGLE FOWL HENS (*GALLUS GALLUS* SUBSP.)

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Among birds, social organization based on aggressive behavior is both widespread and well-documented. Although much of the information dealing with this facet of avian behavior is the result of studies on captive birds, field observations such as those reviewed by Collias (1944) and later by Allee (1950) indicate that these behavioral phenomena are not merely a reflection of artificial confinement.

With an extensive background of both descriptive and analytical information about the social organization of the common domestic fowl, a study of the hierarchical behavior of a closely related species presented itself as a worthwhile venture. C. O. Whitman (1898) voiced the rationale for the study of behavioral phenomena from the standpoint of phylogenetic descent. Recently, Lorenz (1950) has reiterated this point of view. The pioneer attack of this type of study was that of Whitman on the Columbidae, published posthumously in 1919. Heinroth (1910) also followed the phylogenetic point of view in his behavioral analysis of the Anatidae. Behavioral studies of representatives of three closely related genera of grouse by J. W. Scott (1950) are phylogenetic in nature. J. P. Scott (1950) compared the social behavior of wolves and dogs. The behavior of a number of invertebrates has been studied with the view of establishing phylogenetic relationships. The studies of Petrunkewitch (1926) on spiders Wheeler (1923) on a number of species of social insects, Emerson (1938) on the phylogeny of nest construction in colonial termites, and Crane (1949) on the comparative behavior of salticid spiders are noteworthy examples of investigations by students of invertebrate biology. The selection of a species closely related to the domestic fowl for a study of social organization is in line with this approach.

Although the exact relationship between the Red Jungle Fowl *Gallus gallus* subsp. and the domestic fowl *Gallus gallus* L. is not completely clear, the evidence presently available indicates that these forms are closely related. A discussion of this taxonomic problem is outside the scope of this report and the reader is referred to the works of Tegetmeierer (1873), Darwin (1890), Hutt (1949), and McCabe and Deutsch (1952) for information on this point.

The present investigation is of a twofold nature: (1) to contribute to our knowledge of the hierarchical behavior of hens of a previously unstudied species, *G. g.* subsp.; (2) to compare this behavior with that of the closely related common domestic hen *G. gallus* L.

The material to be presented is a portion of a study submitted to the Graduate School of the University of Florida in partial fulfillment of the requirements for the Ph.D. degree. The author gratefully acknowledges the advice and interest of the late Dr. W. C. Allee, former Head Professor of Biology of the University of Florida, under whose supervision this study was carried out. Dr. J. C. Driggers, Associate Professor in the Department of Poultry Husbandry, gave many helpful suggestions concerning the practical aspects of caring for the birds.

ANIMALS AND THEIR TREATMENT

This report is based on a study of four flocks of Red Jungle Fowl hens. These birds were part of a larger colony, containing both males and females, that was developed from a group imported into this area from a fancy-bird breeder in California. The flocks were quartered in wooden chicken houses, each divided into two 8 x 12-foot pens. Extending the length of each pen was a dropping board, 2 feet above the floor and 3½ feet wide. Six inches above the latter were two or three 2 x 4-inch perches. The pens were also furnished with water pails, mash hoppers, and poultry nest boxes. Wood shavings litter covered the dropping boards and pen floor. Each pen opened by a small door to an outdoor yard. The L-shaped yards were 20 feet wide and 38 feet long. Approximately 6 feet above the ground, 2-inch chicken mesh served to enclose all outdoor yards from above.

The partition dividing each house into two pens was constructed partially of a wooden wall and

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frame door with wire mesh covered with burlap completing the division. A small square of burlap covering the mesh of the door was cut out to afford a clear view of the pen floor; only the head of the observer was clearly visible to members of the flock undergoing observation.

Commercial poultry egg-laying mash and water were provided at all times. During observation periods, a mixture of whole grains comprised of corn, wheat, and oats was dropped in a central area of the pen floor. Large plastic wing badges with bold black numbers on a yellow background proved excellent for rapid identification of the birds. Social interactions between individuals were recorded by writing down the particular wing badge number, and the type of aggressive-submissive behavior exhibited. However, a more expeditious and quantitatively accurate method of recording this type of social behavior, used by Banks and Allee (1954), was followed when possible. This technique consisted of recording by voice all observed interactions on a magnetic tape-recorder and transcribing these data after the observation period. The advantage of such a recording method is obvious; the voice of the observer had no apparent effect on the birds. Finally, slow-motion moving pictures of much of the hierarchical behavior observed in this study were taken.

The observation period took the following course. After placing the mixed grains on the floor of the pen to be studied, the observer took a position in the adjacent pen. If the latter was occupied by a flock, it was carefully stimulated out to the yard, and the yard door closed. No attempt was made to force all members of the flock undergoing observation into their pen. Experience indicated that such a procedure could disrupt the normal flock behavior for a considerable period of time. Furthermore, it was found to be unnecessary to lock all individuals of an observed flock into their pen. Motivation for the grains was kept at a high level by feeding only during observation periods. The sound of the grains being dropped on the floor was usually sufficient to attract all birds into the pen, providing the observer had taken his position in the adjoining pen. The observation recording period varied from 10 to 30 minutes.

In the present work the aggressive-submissive interactions between pairs of individuals were characterized by the following objective criteria: aggressive behavior was manifested by pecking, or threatening by a dominant; submissive behavior was evidenced by avoiding movements by the subordinate individual. The peck is an overt action wherein the aggressive individual strikes the contact-mate with the bill. These blows generally fall on the head and neck regions. Threats may be less obvious to the casual observer, but are characterized as ". . . undelivered pecks or instances in which the dominant bird raised its hackle or in an otherwise threatening manner caused the inferior to which this behavior was directed to avoid the threatening bird" (Guhl 1953). Avoidance behavior, exhibited by a submissive individual, ranges from a mere dodging of the head to escape a peck to rapid and quite skillful flight.

Although the level of aggressive behavior is enhanced by the methods used in obtaining the data presented below, social interactions of the same type may occur in the absence of obvious competitive situations. A dominant hen may strike a subordinate while both are merely walking about the pen or yard. On the other hand, it is not the intent of this report to give the impression that the only activity to be seen in penned flocks of Jungle Fowl hens is the display of hierarchical behavior. Other types of activity not mentioned above and incidental to this study include such hierarchically neutral behavior as preening, sand or dust bathing, roosting, random walking and scratching in the litter or soil. The Red Jungle Fowl is an extremely "excitable" bird. When it became necessary to handle the hens, for example, to move individuals from one pen to another, it was found most expedient to make such moves at night after the birds had gone to roost for a few hours.

The data to be discussed below are based on observations extending from July 7, 1953 to November 23, 1954, which totaled 78.3 hours of close watching. Except where indicated, the four flocks of Red Jungle Fowl hens included were composed of sexually mature individuals, ranging in age from four to five months and upwards. The age of the oldest hens in this group was not precisely known; these birds were sexually mature at the time of their arrival in October, 1951. During the period noted above, the hens were assembled in unisexual flocks except for flock 10A into which three males were periodically introduced for breeding purposes.

Table I presents a list of hens comprising the four flocks. Of the twenty-six hens used, twelve were members of two flocks and fourteen of one. Rearranging the birds in this manner allowed for a more thorough study of the hierarchical behavior exhibited by the relatively small number of hens available. A discussion of the effects of this procedure will appear below. The largest flock was 10B, composed of ten hens during the final month of study. Seven individuals were members of flock 10A during the final month of its existence.

Flocks 23A and 23B contained nine and eight hens, respectively. As indicated in Table I, deaths occurred during the study period in flocks 10A and 23B. Post-mortem examinations were performed by Drs. M. W. Emmel and G. Van Ness of the Poultry Pathology Laboratory of the University of Florida. These events will be further mentioned under the following section.

TABLE I. Flock membership

Hen	10A	10B	23A	23B
30	X	..	..	..
196	X	X	..	..
47	X	..	..	X
160	X	X	..	..
189	X	X	..	..
156	X	..	..	..
29*	X	..	..	..
130	X	X	..	..
34*	X	..	..	..
22	..	X	..	..
57	..	X	X	..
12	..	X	X	..
322	..	X	..	..
210	..	X	X	..
106	..	X	..	..
18	..	..	X	X
20	..	..	X	X
86	..	..	X	X
321	..	..	X	..
2	..	..	X	..
17	..	..	X	X
66	..	..	..	X
154	..	..	..	X
158	..	..	..	X
40*	..	..	..	X
38	..	..	..	X

X = member of
*died during observation period.
Inclusive dates of study
10A — 11/24/53 to 3/22/54
10B — 6/14/54 to 11/19/54
23A — 7/9/53 to 11/2/53
23B — 6/14/54 to 11/23/54

A complete tabulation of aggressive interactions for all four flocks will be presented. A separate tabulation of avoids recorded during these observations is not given; such a chart would essentially reveal a reverse-image of that presented by the tabulation of recorded threats. The social organizations will be illustrated in the form of sociograms. Each flock will be discussed briefly and pertinent observations noted in the following section.

OBSERVATIONS

FLOCK 10A

Observations of the hierarchical behavior of this flock extended from November 24, 1953 to March 22, 1954, the group being studied on 74 days for a total period of 21 hours. A sociogram indicating the dominance-subordinance relationships of the nine hens at the end of this period comprising this flock is presented in Figure 1. The social organization exhibited is characteristic of the type based on peck-right dominance. When the birds are ranked according to the number of individuals dominated by a particular hen, the hierarchy approaches a straight line except for the triangular relationships existing among hens 160, 189, and 156. A complete tabulation of the recorded social interactions appears in Tables II and III. Observed social interactions, or pair contacts, between members of this flock totaled 2,072. The two forms of aggressive activity, pecking and threatening, each contributed about equally to the total.

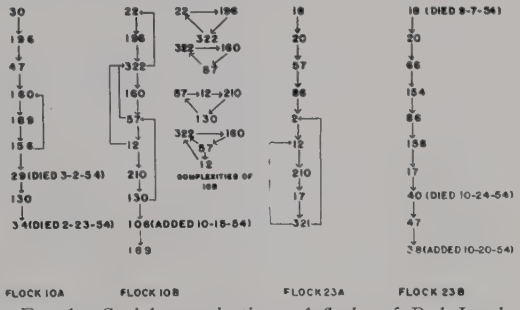

FIG. 1. Social organizations of flocks of Red Jungle Fowl hens. Except where indicated, hens above are dominant to those below.

TABLE II. Aggressive interactions in flock 10A: number of observed pecks

		Subordinate hens									
		30	196	47	160	189	156	29	130	34	Total
Dominant hens	30	..	93	60	48	53	37	45	37	10	383
	196	..	..	52	23	47	38	12	19	17	208
	47	..	..	..	28	13	21	16	26	15	119
	160	..	..	..	..	24	3*	33	23	18	101
	189	..	..	..	..	..	34	29	12	10	85
	156	..	..	..	30	..	..	47	20	31	128
	29	1*	..	1*	..	1*	4*	..	20	23	50
	130	..	..	..	..	..	..	..	..	23	23
	34	..	..	..	..	..	..	..	..	..	0

*Peck-order violation.

TABLE III. Aggressive interactions in flock 10A: number of observed threats

		Subordinate hens									
		30	196	47	160	189	156	29	130	34	Total
Dominant hens	30	..	61	46	33	29	41	21	28	33	292
	196	..	..	63	41	38	45	18	28	12	245
	47	..	..	..	39	28	32	10	41	18	168
	160	..	..	..	..	10	..	19	7	13	49
	189	..	..	..	..	..	12	27	13	22	74
	156	..	..	..	53	..	..	12	21	14	100
	29	..	..	..	..	..	..	..	22	11	33
	130	..	..	..	..	..	..	..	..	9	9
	34	..	..	..	..	..	..	..	..	..	0

The most striking aspect of the hierarchical behavior of these hens is the rigidity characteristic of their relative dominance-subordinance positions. Of the total number of observed pecks, approximately 1% fall into the category known as revolts, or peck-order violations as defined by Holabird (1955). Hen 160, on three occasions, pecked 156, a bird that was clearly its social dominant. One other hen in this flock, 29, committed seven peck-order violations, one of which was directed to hens 30, 47, and 189, respectively, and four to 156. None of these instances of peck-order violations resulted in reversals of dominance. Each was quickly followed by a countering peck or threat by the dominant hen.

One further noteworthy aspect of the tabulation of pecks is the fact that those hens occupying highest ranks in the hierarchy were also observed to exercise the peck-right most frequently. Were the individuals in this flock to be ranked according to the number of pecks delivered, the resulting hierarchy would follow the same order as that presented in the sociogram in Figure 1, with the exception of hen 156, whose numerical record would place her above 189. With respect to the record of observed threats presented in Table III, the trend is in the same direction as that of the pecks, but in this instance the association between numbers of threats delivered and social status is not as close.

As has been noted previously, three males were periodically introduced into this flock for breeding purposes. The effect of this procedure on the hierarchical behavior of the hens, and a report of the breeding behavior observed will be presented in another paper. It should be noted, however, that the data presented above represent observations carried on in the absence of the three males.

FLOCK 10B

Observations of this flock extended from June 14, 1954 to November 19, 1954, for a combined total of 18 hours distributed over 107 days. Originally composed of nine hens, the number was increased to ten individuals with the introduction of 106 on October 15, 1954. A tabulation of pecks and threats is presented in Tables IV and V, respectively. An examination of the structure of the organization as found in Figure 1, reveals a marked departure from a straight-line hierarchy. For the sake of clarity, the complex dominance-subordinance relationships revealed in the sociogram of flock 10B are illustrated individually in Figure 1. Two simple triangular relationships are found, one among hens 22, 196, and 322, and the other among 322, 160, and 57. A third complication is that among 57, 12, 210, and 130. The final deviation from a straight-line hierarchy is an extension of the second triangle referred to above, with the addition of 12, subordinate to 160 and 57, but dominant to 322. The sociogram may be said to represent a geometrical type of peck order (Foreman, D. *in litt.*).

Hen 106 was arbitrarily added approximately four months after the flock was assembled. It should be noted that all resident hens except 189 won peck-right over 106. This fact is of interest for two reasons. At the time of introduction, 106 was four and one-half months old and therefore the youngest individual present. The dominance of 106 over 189 is contrary to findings, to be reported in another paper, on similar introductions wherein the younger of two individuals is generally found to be subordinate to the older of the contact pair. A second consideration is that members of an organized flock tend to win over singly introduced strangers if the introduction occurs in the home pen of the organized flock. The explanation of the dominance of 106 over 189 rests on the fact that the latter became broody late in June and continued in that condition throughout the study. The extended period of broodiness, as

TABLE IV. Aggressive interactions in flock 10B: number of observed pecks

Dominant hens	Subordinate hens: 22	196	160	57	12	322	210	130	106	189	Total
22	..	37	18	23	17	4*	28	18	38	49	214
196	..	..	42	19	32	27	18	11	12	23	184
160	..	..	..	14	27	..	32	40	8	15	136
57	..	..	..	..	38	17	27	1*	29	18	130
12	..	..	..	..	..	30	17	22	21	11	101
322	97	..	83	..	..	..	13	11	15	8	227
210	..	..	..	..	..	..	..	12	12	20	44
130	..	..	..	28	..	..	..	..	17	7	52
106	..	..	..	..	..	..	..	..	..	58	58
189	..	..	..	..	..	..	..	..	..	..	0

*Peck-order violation.

TABLE V. Aggressive interactions in flock 10B: number of observed threats

Dominant hens	Subordinate hens: 22	196	160	57	12	322	210	130	106	189	Total
22	..	58	33	17	23	..	28	21	28	18	226
196	..	..	76	13	15	17	17	31	17	10	196
160	..	..	..	28	32	..	17	36	33	15	161
57	..	..	..	..	18	12	7	..	12	6	55
12	..	..	..	..	..	13	23	8	18	3	65
322	128	..	140	..	..	..	27	18	12	29	354
210	..	..	..	..	..	..	..	12	30	14	56
130	..	..	..	11	..	..	..	..	14	19	44
106	..	..	..	..	..	..	..	..	..	43	43
189	..	..	..	..	..	..	..	..	..	..	0

such, is not important; no males were present for insemination and the eggs layed by 189 were not fertilized.

One of the concomitants of broodiness in other birds, such as the common domestic hen and the pigeon, is a reduction in the secretion of gonadal hormones (Riddle and Bates 1939). This reduction, if such did in fact occur in hen 189, was reflected in a decrease in the aggressive behavior. Collias (1943) found that male hormone, as indicated by comb size, was a major factor in the ability of domestic hens to win initial contests. Such an explanation must remain provisional until endocrine studies are undertaken on the Red Jungle Fowl, but if such were the case, it would offer an interpretation for the success of 106, a young, strange hen, in gaining dominance over 189, a fully adult, long-time resident of the flock. Further support for this reasoning rests on the reversal of dominance-subordinance relations between 130 and 189. The latter held peck-right over 130 when both were members of flock 10A, and during the first week of observation of the present flock. After 189 became broody, 130 successfully challenged her dominance and executed the sole example of reversal in social status found in this study.

The stability of the hierarchy in Red Jungle Fowl hens is further demonstrated by the small number of peck-order violations witnessed in this flock. Hen 22 committed four violations against 322, none of which resulted in alteration of the hierarchy. In addition, 57 pecked 130, her social dominant, on one occasion. This peck-order violation was quickly retaliated by 130. Of the total number of observed pecks recorded during the 18 hours in which flock 10B was studied, only about 0.4% could be classified as being counter to the social organization.

The correspondence between social status and observed aggressive activity is less clear in this flock than it was in flock 10A. The trend, however, remains in the direction of more frequent use of the peck-right in those hens holding high social rank. An interesting exception to this tendency is shown by the record of hen 106. Though dominant only to 189, the total number of pecks recorded for 106 compares favorably with that of 130 and 210, both of which were dominant to three individuals.

FLOCK 23A

A total of 21.2 hours distributed over 65 days was spent in the observation of this flock. Study began on August 9, 1953 and extended to November 2, 1953. A tabulation of the social interactions witnessed is presented in Tables VI and VII for pecks and threats, respectively. A sociogram of the hierarchy so determined appears in Figure 1. It will be noted that this flock is organized in a simple straight-line hierarchy, except for the dominance of 321 over 2 and 12. Aside from these deviations, the hierarchical behavior of these hens is straightforward and typical of the peck-right form of social organization. No peck-order violations were observed.

TABLE VI. Aggressive interactions in flock 23A: number of observed pecks

		Subordinate hens									
		18	20	57	86	2	12	210	17	321	Total
Dominant hens	18	..	152	97	38	26	23	15	43	21	415
	20	..	..	103	76	22	27	34	17	18	297
	57	..	..	..	23	29	29	58	18	78	235
	86	..	..	..	..	23	11	41	14	17	106
	2	..	..	..	..	..	32	21	11	..	64
	12	..	..	..	..	..	..	18	27	..	45
	210	..	..	..	..	..	..	..	13	28	41
	17	..	..	..	..	..	..	..	..	31	31
	321	..	..	..	..	41	22	..	..	..	63

TABLE VII. Aggressive interactions in flock 23A: number of observed threats

		Subordinate hens									
		18	20	57	86	2	12	210	17	321	Total
Dominant hens	18	..	19	39	11	18	21	33	30	25	196
	20	..	..	42	37	47	40	18	28	33	245
	57	..	..	..	29	17	39	41	18	26	170
	86	..	..	..	..	38	29	33	16	52	168
	2	..	..	..	..	..	31	28	41	..	100
	12	..	..	..	..	..	..	22	47	..	69
	210	..	..	..	..	..	..	..	28	17	45
	17	..	..	..	..	..	..	..	..	42	42
	321	..	..	..	..	37	21	..	..	..	58

The alpha hen 18, the oldest female of the colony, exercised her peck-right vigorously and persistently, and contributed approximately one third of the total number of pecks recorded for the flock. The aggressive behavior of 18 was of such a severe nature that some subordinate hens responded to her in an ambiguous manner. Number 18 is the only hen to which subordinates gave the "sex-crouch" as a manifestation of submissive behavior. This behavior pattern is frequently seen in receptive hens in the presence of a male and consists typically of a lowering of the body into a squatting attitude, wings raised and held away from the body; neck, head, and beak extended horizontally above the floor. The sex-crouch was exhibited by 2, 12, 120, and 17 in interactions with 18. Although extremely aggressive, 18 did not appear masculinized, *i.e.*, her comb

was no larger than that of other hens and she produced and incubated normal clutches of eggs.

FLOCK 23B

Study of the hierarchical behavior of flock 23B extended from June 15, 1954 to November 23, 1954, for a total of 18.1 hours of actual watching and recording of behavior distributed over 109 days. Tabulations of the aggressive behavior recorded appear in Tables VIII and IX for pecks and threats, respectively. A sociogram of the organization of this flock, illustrated in Figure 1, reveals a straight-line dominance-subordinance hierarchy. The alpha hen, 18, held her position until September 7, at which time she died of chronic pullets disease. It is interesting to note, in this respect, that although 18 became distinctly less vigorous in all aspects of her observed behavior, between the time this flock was assembled and her death, there were no known peck-order violations directed to 18. During June, 40 was observed to respond to the aggressive approaches of 18 by exhibiting the sex-crouch on two occasions. Following the death of 18, the second-ranking individual in the hierarchy, 20, became alpha hen.

TABLE VIII. Aggressive interactions in flock 23B: number of observed pecks

		Subordinate hens										
		18	20	66	154	86	158	17	40	47	38	Total
Dominant hens	18	..	58	22	31	18	12	28	34	13	8	224
	20	..	..	37	28	47	49	52	46	33	21	313
	66	..	..	..	42	18	31	41	23	14	10	179
	154	..	..	..	..	14	26	17	13	22	7	99
	86	..	..	..	..	..	22	18	22	6	8	76
	158	..	..	..	..	..	..	13	19	23	5	60
	17	..	..	..	..	..	..	..	21	18	11	50
	40	..	..	..	..	..	..	..	..	17	3	20
	47	..	..	..	..	..	..	..	..	..	2	2
	38	..	..	..	..	..	..	..	..	..	..	0

TABLE IX. Aggressive interactions in flock 23B: number of observed threats

		Subordinate hens										
		18	20	66	154	86	158	17	40	47	38	Total
Dominant hens	18	..	17	31	20	17	18	21	23	14	11	172
	20	..	..	72	58	47	60	120	33	41	42	473
	66	..	..	..	51	38	14	23	18	21	31	196
	154	..	..	..	..	49	31	34	28	17	10	169
	86	..	..	..	..	..	33	28	16	18	14	109
	158	..	..	..	..	..	..	47	30	21	17	115
	17	..	..	..	..	..	..	..	31	20	22	73
	40	..	..	..	..	..	..	..	..	21	5	26
	47	..	..	..	..	..	..	..	..	..	18	18
	38	..	..	..	..	..	..	..	..	..	..	0

Approximately one month before observation of this flock was discontinued, 38, a five-month-old pullet was introduced. In this instance, the young, strange individual was defeated in pair-contacts with all resident flock members and assumed omega status in the hierarchy which is the normal, expected outcome of such a procedure. Hen 40 died of lymphomatosis on October 24, 1954. Although she was observed in pair-contact with 38, the newly introduced pullet, on only eight occasions, 40 was clearly dominant over 38.

RELATIVE STATUS IN TWO FLOCKS

As previously noted, twelve of the twenty-six hens used in this study were members of two flocks. The hierarchical behavior of these individuals may be viewed from two aspects: (a) the relative dominance-subordinance relationships of those hens that were both members of the same two flocks, and (b) the status of each such hen in the hierarchy of the two flocks of which it was a member.

Of fifteen pairs of hens, which were later transferred to different flocks, reversal of dominance occurred in only one pair. It is clear from this analysis that once dominance becomes established between any pair of individuals, transfer to another flock or the introduction of new hens into the same pen has no effect on the dominance-subordinance relationships previously determined. The one exception is the case of 189 and 130. When members of flock 10A, 189 was dominant to 130. Approximately three months later, when both individuals were members of flock 10B, 130 became dominant over 189. This reversal in social status has been discussed previously.

The status of each bird in the hierarchy of the two flocks of which it was a member is presented in Table X. The relative position of each hen is given in terms of numbers of individuals dominant or subordinate to a particular bird. In general, there are no striking differences in the status of a given hen in the A flocks, the first set, and the later-organized B flocks. The records of 189 and 47 are exceptional in this respect. The case of 189 has already been discussed and it is of interest here merely to note that when a member of flock 10A, 189 ranked midway in the organization of that flock. Later, when a member of 10B, 189 fell to omega status.

The case of 47 is also worthy of note. When a member of 10A, 47 was dominant to six hens and subordinate only to the alpha and beta members of that flock. On being transferred to 23B, 47 lost initial encounters with all flock members becoming the omega hen of the organization. When 38 was added to 23B, late in the study, 47 won

TABLE X. Social status of hens which were members of two flocks

Hen	Flock	Number dominant to	Number subordinate to	Flock	Number dominant to	Number subordinate to
130	10A	1	7	10B	2	7
196	10A	7	1	10B	8	1
189	10A	4	4	10B	0	9
160	10A	4	4	10B	6	3
18	23A	8	0	23B	8	0
20	23A	7	1	23B	8	0(1)†
86	23A	5	3	23B	4(5)*	3(4)†
17	23A	1	7	23B	2(3)*	5(6)†
57	23A	6	2	10B	6	2
210	23A	2	6	10B	3	6
12	23A	3	6	10B	5	4
47	10A	6	2	23B	0(1)*	7(8)‡

*After addition of 38. †Before death of 18. ‡Before death of 40.

TABLE XI. Flock reorganization scheme (> = dominant over)*

Flock 10B	Flock 23B
Home pen of:	Home pen of:
196 >57, 12, 210, 322, 106	*18* >66, 154, 158, 40, 47
160 >57, 12, 210, 106	*20* >66, 154, 158, 40, 47, 38
130 >57, 106	*86* >158, 40, 47, 38
189 >none	*17* >40, 47, 38
Introduced into 10B from 23A:	Introduced into 23B from 10A:
57 >*189*	47 >none
12 >*130, 189*	
210 >*130, 189*	
Introduced into 10B from surplus pen:	Introduced into 23B from surplus pen:
22 >*196, 160, 130, 189*	66 >*86, 17*
322 >*189*	154 >*86, 17*
106 >*189*	158 >*17*
	40 >none
	38 >none

*See text for explanation. Hens in italics were long-time residents of the pen.

peck-right over 38. This last observation lends support to the generalization that strange individuals added singly to an organized flock tend to lose initial pair-contacts with resident hens.

EFFECT OF HOME "TERRITORY"

Table XI illustrates the composition of the second set, or "B" flocks. Flock 10B was made up of four birds that had been members of 10A. Hens 196, 160, 130, and 189 had long experience with the pen in which they were housed. Into this pen 57, 12, and 210 from flock 23A were introduced. The remaining members of 10B, 22, 322, and 106, were transferred from a surplus, previously unobserved group. To the last six hens, the pen housing 10B constituted a physically strange area. All but 106 were introduced in pen 10B on the evening before observation of this flock was begun.

Flock 23B was similarly composed of four hens that as members of 23A had long experience with the pen. These were 18, 20, 86, and 17. One bird, 47, was introduced from 10A and the remaining five were transferred from the unobserved surplus flock. Except for 38, the hens to which pen 23B was an unfamiliar area were introduced as a group on the same evening.

It is of interest to examine the resulting hierarchies of 10B and 23B to determine whether hens to whom the pen was a familiar area were more successful in winning peck-right than were those individuals to whom the pen constituted a strange territory.

With respect to 10B, we note that 22 won dominance over all four hens that were long-time residents in the pen. Of the remaining introduced birds, 12 and 210 won over two long-time residents and 57, 322, and 106, over one. Among the hens with long experience in this pen, 196 won over five introduced birds, 160 over four, and 130 over two. Hen 189 failed to gain peck-right over any of the introduced birds.

In flock 23B only three of the introduced birds gained dominance over long-time residents. Hens 66 and 154 won over 86 and 17, and 158 became dominant to 17. Hens 47, 40, and 38 failed to win over any of the pen-experienced individuals. Both 18 and 20, long-time residents of the pen, won over all introduced birds (hen 18 died before 38 was added to the flock). Hens 86 and 17 were moderately successful in winning over introduced birds.

The trend indicated by these data is in the direction of success in winning crucial initial contacts associated with familiarity or long-time residence in the given pen. The exceptions, particularly that of 22 in flock 10B, and the small number of cases, prevent a generalization. From information to be reported at another time, it is known that strange hens introduced singly into organized flocks invariably lose to most or all resident hens. The fact that in the present instance, birds were added in considerable numbers on one night may explain the failure of long-time residents to benefit from the advantage of familiarity with the pen and win dominance over all introduced birds.

DISCUSSION

Small flocks of Red Jungle Fowl hens clearly exhibit a social organization or hierarchy. This organization is based on the peck-right type of dominance-subordinance relationship between members of the group. Dominance is manifested by overt behavioral activity such as pecking and threatening. The structure of the social organizations found in the four flocks under discussion ranges from the simple, straight-line hierarchy in 23B to the rather complicated geometrical-type of organization of flock 10B.

The rigidity of dominance relationships among flock members is amply illustrated by the data presented above. A total of 9,279 pecks and threats were recorded during 78.3 hours of observation, extending from July 1953 to November 1954. Of this total, there were only fifteen instances in which an observed aggressive act ran counter to the known dominance-subordinance relationships of the hens. The role of such peck-order violations in the dynamics of hierarchical behavior is incompletely understood (Holabird 1955). These phenomena may indicate conditions of stress preliminary to actual reversal in dominance between members of the contact pair, but there is no evidence from the present study that such is the case. On the other hand, such behavior may simply reflect the rapid movements that are characteristic of the feeding hens. Misdirected aggressive activity under these circumstances seems entirely likely; the rareness of such behavior is mute testimony to the ability of Jungle Fowl hens to recognize their flockmates precisely and rapidly, and to react "properly" in the vast majority of contacts.

The stability of dominance-subordinance relationships in this form is further indicated by the behavior of those hens which were members of two flocks. With one exception such individuals maintained the same relationship to each other in both flocks.

The expression of submissive behavior by the subordinate of a pair-contact has not been stressed in the preceding section. The response of subordinate individuals to pecking or threatening by socially dominant flockmates is such as to increase the distance between the dominant and the interacting subordinate. The latter may move her head away from the dominant or may run or fly out of the feeding area. The form of the avoiding response was of particular interest only in those cases in which subordinate hens exhibited the sex-crouch to an overt aggressive act by hen 18, alpha member of flocks 23A and 23B. Under these conditions, the sex-crouch is an unadaptive response. A hen in this attitude may remain motionless while being pecked repeatedly by the dominant. The sex-crouch so displayed may be an example of a displacement activity. As generally defined by Thorpe (1951) a displacement activity is "the performance of a behaviour pattern out of the particular functional context of behaviour to which it is normally related." The sex-crouch may be considered as a typical response given by a sexually receptive hen when pecked by a cock approaching from behind. After the first sex-crouch was noted in flock 23A, care was exercised to observe the manner of approach of hen 18 when interacting with subordinates. Recall that 18 was a particularly aggressive individual. She frequently chased subordinates for some time before returning to the feeding area. It is interesting to note that four of the five cases of sex-crouch responses to 18 occurred when the latter was in pursuit of the subordinate individual and was thus approaching vigorously from behind, as would a male attempting to mount. The small number of these observations, however, demands cautious interpretation. Pursuit by dominants did not invariably, or even frequently evoke the sex-crouch by the subordinate individual.

It would be of interest, at this point, to compare the hierarchical behavior of Red Jungle Fowl hens with that of common domestic hens. Beginning with the published works of Schjelderup-Ebbe (1913, 1922, 1935) and extending through the investigations of Allee and his students, a rather considerable body of information concerning social organization in common domestic fowl is available. The reviews of Allee (1950) and Guhl (1953) represent the latest summaries of this field and the reader is directed to these papers for documentation of many of the comparative statements to follow.

There is no essential difference between the type of social organization exhibited by small flocks of the two forms. In both, the hierarchy is based on peck-right dominance. Social relationships between individuals are determined during initial pair-contacts and are of an enduring nature. The structure of the hierarchy varies from the simple straight-line type to the complex geometrical peck order in which complicated triangles of dominance are encountered.

The manner in which dominance is exercised is the same in both Red Jungle Fowl and common domestic hens. Pecking and threatening are the primary manifestations of dominance behavior. Fighting rarely occurs in organized flocks of domestic hens. It was never encountered in the present study. The activity of subordinate members of interacting pairs is similar and varies from slight avoidance movements to rapid evasion of the dominant.

In a study designed to test the ability of domestic hens to become part-time members of a number of flocks, Douglis (1948) noted that dominance relations between pairs of test hens, moved from one flock to another, did not change, even though one member of the pair may have attained higher status in a given flock than did its transfer partner. This finding is paralleled, to a degree, in the present study by the behavior of those hens that were members of two flocks.

There are approximately 45 standard breeds of domestic fowl (Am. Poultry Assoc. 1945). Each breed may, in turn, be divided into a number of varieties. The varieties are frequently further divided into strains. It is obvious that domestic fowl have undergone intense selection by poultry breeders for centuries. Among the many factors which have been under selection are color patterns, feather form, body size and conformation, meat and egg production, and broodiness. It is therefore of interest that in those breeds, varieties, and strains which have been studied, no basic differences in the manifestation of hierarchical behavior have been found. There are variations between breeds and between strains of a single breed variety with respect to levels of aggressiveness and other minor characteristics (Potter 1949; Holabird 1955), but is it noteworthy that despite long and intense artificial selection for other factors, few important differences in the expression of hierarchical behavior are known among females of *G. gallus*.

In conclusion of this part of the discussion it may be said that no basic distinction is found between the social organization of flocks of Red Jungle Fowl hens and common domestic hens. Indeed, insofar at its hierarchical behavior is concerned, the Red Jungle Fowl hen does not differ from the common domestic hen to any greater degree than certain breeds of domestic fowl are known to differ from each other.

The fact that social organization in Red Jungle Fowl hens is basically indistinguishable from that of the closely related domestic hen is an indication of the fundamental nature of this behavioral phenomenon. Collias and Taber (1951) noted a social hierarchy based on peck-right dominance in free-ranging ring-necked pheasant hens, another species of the family Phasianidae in which both Red Jungle Fowl and domestic fowl are classified.

Such a widespread and persistent behavioral characteristic as the social hierarchy is not without evolutionary significance. It has been suggested (Allee and Guhl 1942; Collias 1944; Guhl and Allee 1944; Allee 1950) that groups of animals organized into hierarchies based on dominance-subordinance relationships may more successfully compete or cooperate at the group level than they would if unorganized.

It should be emphasized that this study was conducted under conditions which were somewhat restrictive to the birds. It would be of interest to know the nature of the hierarchical behavior shown by Red Jungle Fowl hens in their natural environment. Descriptions of the natural history of the Red Jungle Fowl, such as that of Beebe (1926), are not helpful in this respect. However, a recent report by Tordoff (1954) on the social organization of the red crossbill provides some insight into the present problem. A flock of this passerine species was observed in the field and its hierarchical behavior noted. After trapping, the flock was observed under restricted conditions, and it was concluded that the only noticeable change was an increase in the display of aggressive-submissive activity.

Summary

The social organization of twenty-six Red Jungle Fowl hens comprising four flocks was studied for a total of 78.3 hours, extending from July 7, 1953 to November 23, 1954. A social hierarchy based on peck-right dominance relationships was found in each flock. Only one case of reversal of dominance was encountered. Other evidence of stability of social status stemmed from the unchanged dominance-subordinance relations between hens that were members of two flocks. There was some association of higher social status with long-time residence in a given pen when the hens were regrouped. These findings permit comparison with the well-known hierarchical behavior of the closely related common domestic hen. This comparison revealed no basic difference in the manifestation of social organization in the two forms.

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REGENERATIVE BEHAVIOR AND SOCIAL HOMEOSTASIS OF TERMITES

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The social system of termites exhibits numerous attributes of the individual organism. Division of labor and integration between the component individual parts, the specialization of parts for reproduction of the whole in contrast to those that serve nutritive or protective functions, the sterility of the "somatic" cells or castes, structural symmetry of the whole system, genetic continuity between generations of whole systems, and other resemblances may be mentioned (Emerson 1939, 1952). To these supraorganismic attributes is added the capacity to regenerate as illustrated by the present examples.

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A question arises concerning the broad general function that relates the organism and the social supraorganism. If significant analogies occur between the physiological unit and the social unit, there must be a common principle that relates the two. It seems to the author that the general function of both division of labor and integration within a unit system composed of specialized parts is to be found in Cannon's concept of homeostasis which may be defined as the self-regulation of optimal conditions of existence and survival. "Self" refers to the unit system at any level of integration. "Regulation" involves feed-back mechanisms, whether biochemical, biophysical, or behavioristic, that operate to decrease excess and to increase any important factor deficient for the living processes of the particular system, so that there is a narrower fluctuation around an optimum than would occur without the regulating mechanism. "Existence" is the development and maintenance of the system at a functional level including replacement of depleted or lost parts by

regeneration, and replacement of whole mortal units by reproductive processes. Improved homeostasis has survival value, so that natural selection produces an evolutionary direction for each system. Integrative levels of biological unitary systems may be genes, whole chromosomes, cells, multicellular individuals, colonial individuals, metameric individuals, metamorphic individuals, aggregations, sex pairs, family units, social units, biocoenoses, communities, and ecosystems. Each has internal homeostatic mechanisms, and each evolves improved homeostasis in time. Homeostasis of one level of individuality may regress as the unit becomes part of a more inclusive system that regulates conditions better than its parts alone. The optimum for one factor is not necessarily the optimum for another, so competitive balance, dominance, and compromise are found in every organismic system. Loss of one part or function is more than made up by the whole system that survives and evolves.

Termite Nests

The behavior of termites is expressed tangibly in nest structures that provide data for certain types of analysis and synthesis not commonly available to comparative psychologists (Schmidt 1955b). Some building behavior is found in the nests of all termites. The reproductive pair constructs a covering seal over the initial nesting cavity following the colonizing flight. The working nymphs of the lower termites, and the workers of the higher termites make partitions between the cells or chambers of the growing nest. These constructions may be made of comminuted wood, particles of soil, or pieces of excrement, glued together by saliva or moist excrement. Many of the higher termites, particularly species of Termitidae, construct conspicuous mounds on the surface of the ground, arboreal nests attached to tree trunks or branches, or more or less definitive subterranean nests. These nests are usually built of carton, a combination of dirt or wood with organic secretions or excretions. Each species may use a distinctive material, or the material may be characteristic of a large taxonomic group. It may be wood carton (*Nasutitermes*), dirt carton (most Termitidae), or excrement with little additional external material (*Crepititermes, Apicotermes*). The Macrotermitinae use excrement to form elaborate fungus gardens.

The nest structures have a variety of forms and details of architecture (Grassé 1937, 1939; Emerson 1938; Grassé and Joly 1941; Desneux 1948, 1953; Grassé and Noirot 1950; Schmidt 1955a). *Cubitermes* (Termitinae) constructs mound nests in the savannas and forests of Africa and, in regions of heavy rainfall, these dirt carton nests may be capped with one or more umbrella-shaped coverings that shed rainwater (Figs. 1, 2). When free on the ground surface, the nests are radially symmetrical structures with a column of a few centimeters to more than sixty centimeters in height, a column diameter from a few centimeters to thirty centimeters, and a cap diameter of a few centimeters to fifty centimeters. The cap extends beyond the circumference of the column and sometimes is edged with finger-like prolongations that

Fig. 1. Mushroom-shaped nest of *Cubitermes sankurensis* Wasmann in the savanna of Sona Mpangu, Belgian Congo. Note the new construction added on top of the older cap.

Fig. 2. Mushroom-shaped nests with caps on nest on a tree trunk of a single colony of *Cubitermes finitimus* Schmitz in the rainforest at Camp Putnam, Epulu River, Belgian Congo. Note the rain-shedding prolongations of the edges of the caps and the gradations from the free radially symmetrical mound to the series of semicircular caps on the tree trunk nest.

also function to shed rain (Fig. 2). The column may be cylindrical or it may be formed of two portions, a wider upper portion with many inhabited chambers, and a narrower supporting stalk with tunnels leading up from the ground (Emerson 1938, p. 273, fig. 11). The parental pair of the colony is usually found at the base of the inhabited column somewhat above or near the ground level. A distinctive royal cell is not characteristic of *Cubitermes* nests, but the chamber inhabited by the royal couple may be a little larger than the other chambers. The eggs and young are usually found in the lower chambers of the column near the royal cell.

This mound type, because of its form, is often called a mushroom-shaped nest. It is characteristic of many species of *Cubitermes* in regions of heavy rainfall, but other species of the same genus in periodically dry savannas and steppes may not build the umbrella cap over the top, and the same species that builds a cap in wet areas may not build one in drier portions of its range. Even with this variation, however, only species of the genus *Cubitermes* build typical mushroom-shaped nests, so that the capacity to react in this manner must be determined by genetic factors. It should be emphasized that the colonizing pair never constructs a nest but only seals the original excavated chamber. The workers developing from the eggs laid by a queen inherit their capacity to build the nest characteristic of their species and genus with no possibility of learning or imitating the behavior of the workers that built the nest or nests from which the parental pair emerged at the beginning of the colonizing flight. The construction behavior of the workers must be considered instinctive and inherited and may be as characteristic of a species, a genus, or a subfamily as are the structural characters that are used for taxonomic description and phylogenetic inference. In the evolution of nest-building behavior by sterile workers, no Lamarckian mechanism is possible (for a contrary interpretation, see Bugnion, 1927). Like anatomical stuctures during growth, behavior during the building of the nest may be modified by the environmental conditions to some extent without, of course, changing the genetic factors or gene patterns that pass through the reproductive cells connecting generations of the same species. Anatomical form and behavior pattern may be presumed to have a basic analogical similarity that can be recognized in phylogenetically related taxonomic categories. In other words, behavior in these cases indicates the same general genetic background exhibited by anatomy. It is subject to the same sort of direct environmental influence of the habitat, and the indirect environmental influence of natural selection on the genetic configuration.

FIG. 3. Chevron-shaped rain-shedding hollow ridges above a nest of *Procubitermes undulans* Schmitz on a tree trunk in the rainforest at Camp Putnam, Epulu River, Belgian Congo.

FIG. 4. Nest of *Cubitermes intercalatus* Silvestri on a tree trunk in Kalina Woods, Leopoldville, Belgian Congo. Note the numerous irregular semicircular caps on the nest surface.

The behavior in the case of termite nest construction is the result of the combined and accumulative actions of thousands of individual workers. The reproductive and soldier castes do not take part in the building behavior after the establishment of the original chamber. Each *Cubitermes* worker brings its bit of material to the place of construction, works it into position with its head and mouthparts, moistens it during the process

with salivary secretions, excretes a droplet of mud-like excrement on the newly placed piece, and leaves the site. Another worker brings its bit of material and places it on top of the preceding piece, and thus the nest is slowly formed. The worker building in one portion of the nest will not return to precisely the same place, but each will react in a given microspatial environment in such a similar way that the nest as a whole exhibits the particular characteristics of its species. The species behavior may be seen in the walls of the cells or chambers, in the openings between cells, in the arrangement of cells, in the form of the royal cell, in the size and shape of the external nest form, in the constituency of the material used, and in the ecological position of the nest. Additions are made during the growth of the colony possibly in response to population density. Normal construction usually takes place at night when atmospheric humidity is high (Fig. 1).

Some species of *Cubitermes* inhabit rainforests, and a few may build their capped nests on the sides of trees rather than free on the ground surface (Fig. 2). In such cases, numerous caps may be built one above the other with the appearance of a series of inverted saucers. These may be fairly large and regular in some species (Fig. 2; Emerson 1938, p. 275, Fig. 12), or there may be a multiple number of irregularly placed caps in other species (Fig. 4). The same species may build a free capped mound or a series of caps on the side of a tree (Figs. 2, 6). The free nests may have two or more regularly spaced caps, or a series of irregular caps (Fig. 5).

Nest Regeneration

The nest of *Cubitermes intercalatus* Silvestri (Fig. 4) was found in second growth woods along the bank of the Congo River at Pointe Kalina on the edge of Leopoldville, Belgian Congo. The edge of each cap was more or less semicircular, and the base of each cap connected with a thick portion of the nest that was built over the tree to a depth of eight to thirty centimeters, becoming thinner near the top about 120 centimeters above the ground level on the tree trunk. On April 5, 1948, the queen was removed and the lower half of the nest was destroyed. The queen was in a cell about 30 centimeters above the ground level and near the tree trunk about 30 centimeters from the surface. The king and queen had obviously moved to this position in the nest following the early building of the nest by the workers. The nest had thick walls and fairly large chambers, but the queen cell was not particularly large although the cell wall seemed a little thicker than the surrounding walls in the immediate vicinity.

After a trip to the interior, this nest was again observed on June 14, 1948, exactly 10 weeks later. The remaining part of the nest on the tree trunk had been repaired at the broken edges (Fig. 5) and was occupied by workers and soldiers. A free radially symmetrical nest had been regenerated from the soil galleries by the same termite colony (Figs. 5, 6). This regenerated nest was about 40 centimeters high with a circular cap on top about 25 centimeters in diameter and also with several partial caps with irregular edges on the columnar portion.

This reconstruction of a symmetrical column and caps is called regenerative behavior. The repair of a damaged nest is referable to the same

Fig. 5. Regenerated free nest ten weeks after the destruction of the lower half of the nest in Fig. 4. Note the prolongations from the repaired portion of the broken nest.

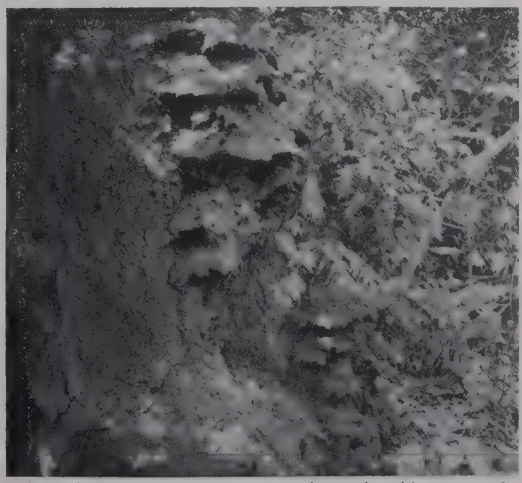

Fig. 6. Regenerated free nest from the side ten weeks after the destruction of the lower half of the nest in Fig. 4.

category of behavior. In this particular case, a completed structure was built by the colony. It happened to start from the soil sufficiently far from the base of the tree to allow the formation of an entire circular cap in contrast to the partially circular caps on the tree trunk nest.

Probably the best case of regenerative behavior was that studied by Hingston (1932). He removed 18 rain-shedding chevron-shaped solid ridges from the tree trunk above a nest of *Constrictotermes cavifrons* Holmgren in British Guiana. Four weeks later, the workers started to repair the "eaves" and at the end of six weeks had regenerated eight when Hingston left the site. This is a remarkable example, but Hingston incorrectly interpreted the behavior as intelligent when the species specificity of the nest denotes instinctive behavior (Emerson 1938). A similar field experiment was attempted by the author on rain-shedding hollow ridges above a nest of *Procubitermes undulans* Schmitz (Fig. 3) at Camp Putnam in the Ituri forest of the Belgian Congo. No regeneration occurred during the six days available for observation following the destruction of the ridges.

The use of the term "regeneration" for social behavior producing a nest reconstruction may be questioned. Webster's Dictionary gives the biological definition of the word regeneration as "the reproduction or regrowth of a part which has been lost or destroyed." The physiological meaning refers to tissue growth, cell growth, or the regeneration of substances within a cell. The regeneration of a nest is extra-protoplasmic, so it is not physiological in the strict sense, but it is the result of behavior that meets the general biological definition of the term. Of course, one would not expect homologous mechanisms to be operating in these widely different types of regeneration. The similarity is not homologous, but is analogous because a functional system is restored.

Social Homeostasis

The place of regenerative behavior can now be seen in the broad perspective of biological processes and evolution. And the principle of analogous function is seen to result from natural selection of many different mechanisms with independent phylogenetic origins. Physiological regeneration of the apical end of an individual *Hydra* or an individual *Planaria* obviously results from very different mechanisms than does the behavioristic regeneration of a capped termite nest, but a similar analogical function is accomplished in the self-regulation of optimal conditions of existence and survival. We must then ask what the homeostatic function of the regenerated *Cubitermes* nest is. We should not expect, at this stage of scientific knowledge, to detect all of the many factors that are regulated, nor all of the mechanisms that operate in this regulation through time, but some may be indicated.

Termite nests homeostatically regulate several factors that contribute to the health and maintenance of the colonies and of the species. The nest wall serves as a barrier to predators in a manner analogous to the shell of a turtle or armadillo. This is demonstrated by the rapid decimation of the termites, usually by ants, when the nest wall is broken open; and by the defensive ring of soldiers that has often been observed around the edge of a nest opening (Allee *et al.* 1949, p. 426, Fig. 149). The soldiers gather at a break in a manner analogous to the concentration of phagocytes in the vicinity of a wound in a mammal. Specialized predators on termites are adaptively adjusted to overcome the nest defenses. Analogous fossorial forefeet have convergently evolved in the monotreme spiny anteater of Australia, the marsupial anteater of Australia, the pholidote scaly anteaters or pangolins of Africa and the Orient, the tubulidentate aard vark of Africa, and the edentate anteaters of the neotropics. Weak laboratory colonies of termites are often invaded by mites and molds that seem gradually to cause the death of the colony. The typically clean appearance of the inhabited nests of termites in nature indicates a homeostasis of sanitation within the nest structure. The Kalotermitidae, particularly *Cryptotermes,* deposit particles of excrement in specially selected portions of the nest excavations in wood.

Regulation of the food supply is indicated by the storage and concentration of gathered food. The author has observed storage of leaf bits in the underground nests of *Syntermes snyderi* Emerson, of cut lengths of grass in the mound nests of several species of *Trinervitermes,* of stripped lengths of plant epidermis in the underground nests of *Anacanthotermes ochraceus* (Burmeister), and of a rich mass of organic matter at the base of the arboreal nests of *Constrictotermes cavifrons* Holmgren. The function of the fungus grown on elaborately constructed fungus gardens by nine genera with 276 known species of the Macrotermitinae is under debate at the present time, but it is the author's opinion that food cultivation by these termites is also homeostatic. It is difficult to believe that such a complex behavior could have evolved over millions of years without an important nutritive function.

The construction of a royal cell and the concentration of eggs and young nymphs in nurseries

also suggest controlled conditions in special portions of the nest.

The capped nest of *Cubitermes* rather obviously sheds rain water and prevents erosion and flooding. Evolutionary convergence of rain-shedding structures in termite nests of different subfamilies is to be found in the nests of *Constrictotermes cavifrons* Holmgren (Nasutitermitinae) in British Guiana, *Amitermes excellens* Silvestri (Amitermitinae) in British Guiana, and *Procubitermes ueleensis* Sjöstedt [= *P. niapuensis* Emerson] (Termitinae) in the Belgian Congo (Emerson 1938). The rain-shedding structures above the nest of *Procubitermes undulans* Schmitz (Fig. 3) are doubtless a case of homologous behavior compared to those of *P. ueleensis* (Emerson 1938, p. 275, fig. 13), and it seems probable that these chevron-shaped ridges have a degree of homology with the caps on the nests of *Cubitermes*. The two genera are taxonomically very close with *Procubitermes* exhibiting a slight phylogenetic advance over *Cubitermes* in the morphology of the soldier mandibles. These examples give evidence that one factor of the environment that is socially self-regulated is rain-water. Phylogenetically convergent analogues in similar habitats strongly indicate the evolution of adaptive behavior by means of natural selection of integrated social systems.

Internal nest humidity is probably a most important homeostatic factor. The studies of Fyfe and Gay (1938) on nests of *Nasutitermes exitiosus* (Hill) in Australia indicate the regulation of this vital condition in the external environment of the individual termites without, of course, precluding the homeostatic regulation of water within the insect body. They showed that relative humidity varied from 92 per cent to 98 per cent in the nest interior when the nest temperatures varied from 11.4°C to 36.8°C.

Behavior may be involved in orientation and movement toward high humidities in a humidity gradient. Experiments by the author on responses of termites and termitophiles in Panama to humidity gradients are listed in Table I. A humidity gradient modified from the design of Williams (1934, p. 47, fig. 8A), was constructed in 1935 on a brass base with sealed brass walls two and one-half centimeters high forming seven approximately square chambers, each nine centimeters in middle minimal diameter, and each connected to the adjoining chamber or chambers at the corners by an angular passageway two centimeters wide. The passageway was made between the chamber wall and an inserted partition three centimeters long joined to the wall near the junction of the two chambers. The passageways acted as buffers to the rapid diffusion of water vapor through the gradient and alternated in position so that the path followed by an insect was sinuous from one end of the gradient to the other. The five middle chambers each had passageways connected to the two neighboring chambers, but the end chambers each had only one such passageway. Anhydrous calcium chloride in fine crystalline form was placed in a small round glass container two centimeters in diameter and one and one-half centimeters high in one end chamber, and a similar glass container with cotton soaked in standing water was placed in the opposite end chamber. A plate-glass cover was placed over the whole series of chambers and carefully sealed around the exterior edges with petroleum jelly.

The per cent relative humidity was not measured directly except in the high-humidity end chamber where the presence of condensed moisture on the glass above the water-soaked cotton indicated dew point and 100% relative humidity. The drying capacity of anhydrous calcium chloride was tested in a large two-quart Mason jar with a hair hygrometer calibrated with a sling psychrometer. The relative humidity decreased from 94% to 30% in one hour, and from 30% to 25% in the next hour. It reached 17% in twenty-one hours and remained at 17% for twelve days. Considering the water vapor diffusing from the high-humidity chamber in the gradient and the water evaporating from the living insects, it seems reasonable to suppose that a gradient becomes established in the chambers approximating 30%, 42%, 54%, 65%, 77%, 89%, and 100%. The reacting insects in the gradient showed a response in about a half hour. Conservatively, the error between the actual and the estimated per cent relative humidity for each chamber did not exceed plus or minus 10%. It may be possible to construct better humidity gradients with other methods (Solomon 1945, 1951).

Besides the inability to determine accurately the actual relative humidity of each chamber during an experiment, several other factors should be considered in evaluating the reported experiments (Table I). The middle chambers had two exits, each two centimeters in width, while the end chambers had one such exit each. There was thus some tendency for the insects to bunch together at each end (note the distribution of *Armitermes chagresi* Snyder at the end of two experiments). Termites are not repelled by other termites but are attracted by humidity, chemical, and tactile responses. Odor trails were eliminated by washing the gradient apparatus in alcohol between experiments, but "contagious" distribution during

TABLE I. Responses of Panama termites, termitophiles, and ant lions to a humidity gradient. No. = Number of individuals placed in gradient.

* = All individuals placed in middle chamber at beginning of experiment.
† = Individuals distributed equally in chambers at beginning of experiment.
N = Large nymphs. S = Soldier caste. W = Worker caste.
Hours = Hours between start and end of experiment.

Species	No.	Caste	Hours	Relative Humidity							
				30%	42%	54%	65%	77%	89%	100%	Mean %
Termites with high humidity response											
Termes panamaensis	100*	W	8	0	0	0	0	0	0	100	100.0
Termes panamaensis	15*	S	8	0	0	0	0	0	0	15	100.0
Termes hispaniolae	105†	W	23	3	1	0	1	0	7	93	94.4
Nasutitermes nigriceps	15*	W	8	0	0	2	0	0	2	11	92.4
Nasutitermes nigriceps	15*	S	8	0	0	0	1	1	8	5	90.3
Nasutitermes columbicus	105†	W	29	4	7	2	4	5	1	82	90.1
Nasutitermes columbicus	7†	S	29	0	0	1	0	1	0	5	90.0
Amitermes foreli	11*	W	24	0	0	0	0	5	2	4	87.5
Amitermes foreli	113*	S	24	0	2	2	35	9	3	62	85.2
Termites with median humidity response											
Armitermes chagresi	140†	W	29	39	11	5	6	7	4	68	71.3
Glyptotermes rotundifrons	98†	N	28	19	3	25	0	17	7	27	68.1
Cryptotermes dudleyi	98†	N	23	0	19	36	2	15	17	9	65.7
Heterotermes tenuis	105†	W	27	37	6	4	2	4	42	10	64.3
Orthognathotermes wheeleri	140†	W	24	38	16	4	21	15	26	20	63.3
Glyptotermes rotundifrons	98†	N	18	17	23	8	7	16	10	17	63.1
Cryptotermes longicollis	7†	S	28	2	1	0	1	2	0	1	60.1
Armitermes chagresi	140†	W	23	58	17	9	5	3	3	45	59.0
Cryptotermes longicollis	98†	N	28	28	7	13	13	25	7	5	58.5
Orthognathotermes wheeleri	140†	W	8	55	14	5	6	33	8	19	57.7
Heterotermes tenuis	44*	W	10	5	18	3	9	3	0	6	56.5
Heterotermes tenuis	12*	S	10	3	2	1	4	0	1	1	56.4
Termites with low humidity response											
Neotermes holmgreni	14†	S	58	7	2	1	0	2	0	2	50.1
Neotermes holmgreni	140†	N	58	67	30	12	3	13	4	11	46.9
Heterotermes convexinotatus	50*	W	23	31	9	3	1	2	1	3	41.6
Termitophiles											
Atelura (Host: N. nigriceps)	8*	—	8	0	0	0	0	0	0	8	100.0
Termitocola cylindricornis (Host: N. nigriceps)	8*	—	8	0	0	0	1	1	0	6	92.7
Termitaradus (Host: H. tenuis)	12*	—	10	3	1	1	2	0	3	2	65.2
Ant Lions											
Myrmeleon larvae	28†	—	26	13	6	6	1	1	0	1	43.1

an experiment could not be eliminated. Grouping of individuals was particularly noticeable in *Neotermes holmgreni* Banks. In the case of the response of the ant lion larvae, *Myrmeleon,* each individual was tactually repellent to others, so that they were individually spaced with some mortality resulting from combats as they congregated in the dry chamber. Termites are sensitive to dry air and mortality from this cause was obvious in all of the experiments. Margaret Strickland (1950) has demonstrated differential toleration to drying in different species of *Reticulitermes.* This factor was not systematically measured in the experiments here reported, but at the end of each experiment a higher proportion of termites was dead in the dry chambers with a generally observed gradient in mortality correlated with the humidity gradient. The high humidity chamber nearly always had a higher proportion of healthy living termites at the end of an experiment than the dry chamber, even in those cases in which the termite species indicated an orientation toward the dry end (*Heterotermes convexinotatus* (Snyder)). Only *Glyptotermes rotundifrons* MS, *Neotermes holmgreni* Banks, the lepismid *Atelura,* and the staphylinid *Termitocola cylindricornis* Seevers, did not show any tendency to die in the dry end of the gradient. It is possible that the accumulation of carbon dioxide in the sealed gradient had some effect on mortality in the longest experiments. The large chambers with smooth brass floors and walls and a glass cover were considerably different from the natural nest chambers of the termites, and doubtless contributed to a "nervous restlessness" during the experiments. Weakness of a termite was observed in one case at two and one-half hours, and was usually detected for a few individuals after five hours. Death of one individual was observed in one case at three and one-half hours, and death often occurred after five

hours, but not before the insect had had ample opportunity to respond to the humidity differential. No responses were observed that might be attributable to temperature or light differences. These various factors tended to interfere with the simple response to humidity alone that the experiments were designed to demonstrate. However, the response to humidity was sufficient to demonstrate clearly a reaction to this factor in several species.

No significant distinction in response was observed between soldiers, workers, or working nymphs of the same species. The termitophiles tested reacted as did their host termites. Ant lion larvae, with an anticipated response to dry conditions, were tested for comparison to termites and termitophiles. Most of the species tested came from the rainforest of Barro Colorado Island, but *Amitermes foreli* Wasmann came from sparsely wooded savanna near Pacora, R.P., *Heterotermes convexinotatus* (Snyder) came from sparsely wooded savanna near Anton, R.P., *Cryptotermes dudleyi* Banks came from a carpenter shop in Ancon, C.Z., *Cryptotermes longicollis* Banks came from low somewhat dry woods on Ancon Hill, C. Z., and the 44 workers and 12 soldiers of *Heterotermes tenuis* (Hagen) with associated hemipterous termitophiles, *Termitaradus,* also came from Ancon Hill, C. Z.

All of the species with definitive arboreal or mound nests showed a response to high humidity. Those termites that are classified as responding to median humidities actually showed no statistical response to humidity at all and are better classified as neutral to a humidity gradient. These termites are either dry-wood Kalotermitidae or are Rhinotermitidae or Termitidae that live in decaying logs or build ill-defined nests in the ground, usually showing no special structure above the ground level. It was rather surprising to find two species of termites that showed a statistical response to the dry end of the gradient. *Neotermes holmgreni* Banks is a log-inhabiting kalotermitid of the rainforest that belongs to a genus that is often classified as a damp-wood termite. *Heterotermes convexinotatus* (Snyder) is a rhinotermitid that lives in somewhat more arid regions than its congener, *H. tenuis* (Hagen). Although it moved to the dry end of the gradient, the specimens died earlier in the dry end than in the humid end, and it is doubtful that the species can tolerate a dry microclimate in nature. It may be concluded from the experiments with a humidity gradient that those species tested that build definitive nests also orient to high humidities, and it may be presumed that the inhabited nest structures maintain an optimum high humidity.

Temperature may be homeostatic in some nests. However, careful studies of temperature in mounds of *Nasutitermes exitiosus* (Hill) in Australia by Holdaway and Gay (1948) only indicate a buffering effect of the nest on environmental temperatures and a higher temperature due to the metabolism of the termites. Nest temperatures are somewhat more stable than the external shade temperatures in arboreal nests of *Nasutitermes corniger* (Motschulsky) in Panama, but direct radiation from the sun will produce higher temperatures than the environment (Emerson 1938). In these cases the temperature control is not marked, and environmental temperature as such is probably of little importance in the life of the insects in the tropics. In the case of *Amitermes meridionalis* (Froggatt) of tropical Australia, the striking orientation of the nests to the meridian probably produces a stabilization of temperature within the nest (Emerson 1938, pp. 266, 268, figs. 7, 8; Allee *et al.* 1949, p. 428, figs. 150, 151). Temperature has an effect upon humidity, so possibly temperature regulation has evolved through selection toward a homeostasis of humidity within the nest.

Actually, mound nests and arboreal nests probably have a greater variation in their internal temperature and humidity than the soil at moderate depths below the surface, and many termites nest in subterranean habitats, coming to the surface only for foraging and for their colonizing flight. Variations in soil water must be great in some localities and mounds probably provide a vertical gradient that allows the population to choose the optimal conditions.

The question occurred to the author whether carbon dioxide might not be an important factor in the function of nest structures and in the habitat of termites. With this idea in mind, measurements of the percentage of carbon dioxide per volume of air were taken in various situations in the vicinity and inside the nest of *Cubitermes intercalatus* that exhibited regenerative behavior (Table II). The apparatus for measuring carbon dioxide percentages in air samples in the field was devised by Dr. Morris S. Kharasch. A gas sample was taken from the soil, nest, or air by means of gravity suction with distilled water into a gas sample cylinder with a volume of 195 cc. Standard hydrochloric acid solutions were made from constant boiling HCl, and sodium carbonate solutions were standardized from them. The volume percentage of carbon dioxide is calculated from a 5-cc solution of 0.00149 molar Na_2CO_3 and

0.00149 molar HCl equivalent to 0.1% CO_2. The gas sample was dissolved by shaking in 5 cc of sodium carbonate solution for five minutes with a phenolphthalein indicator added prior to titration. This solution was then titrated with a measured quantity of hydrochloric acid solution. The titration difference was multiplied by 0.02. Calculations are based upon a gas temperature of 38°C and a gas pressure of 760 mm. Corrections for temperature and barometer readings in the field were found to be negligible.

TABLE II. Percentage of carbon dioxide per volume in different samples of air taken at Leopoldville, Belgian Congo, 307 meters altitude, barometer readings 727.2-729.5 mm., June 1948.

Sample 1. 30.5 cm above ground surface in second-growth woods.
Sample 2. Ground surface under leaf debris in second-growth woods.
Sample 3. 5 cm below ground surface in second-growth woods.
Sample 4. 30 cm below ground surface in second-growth woods.
Sample 5. 15.24 cm below ground surface in exposed grassland.
Sample 6. 15.5 cm above ground and 15.24 cm deep inside base of regenerated mound of *Cubitermes intercalatus* in second-growth woods.
Sample 7. 3.5 cm above ground and 15.24 cm deep inside base of regenerated mound of *Cubitermes intercalatus* in second-growth woods.
Sample 8. 15 cm above ground and 7.5 cm deep in nest of *Cubitermes intercalatus* on side of tree in second-growth woods.

Sample	Shade temperature degrees centigrade	Microniche temperature degrees centigrade	Percentage carbon dioxide
1.....	31.4	31.4	0.030
2.....	26.1	23.9	0.048
3.....	27.8	23.9	0.082
4.....	29.4	24.2	0.198
5.....	32.2	30.0	0.090
6.....	30.0	27.9	0.052
7.....	30.0	26.7	0.162
8.....	30.6	26.1	0.920

It will be noted (Table II) that the carbon dioxide concentration increases in the environment of the nest from lowest concentration in the air above the surface to greatest concentration in the deeper soil layers. Likewise, within the small regenerated nest, the upper strata had a lower concentration of carbon dioxide than the lower strata a little above the ground level. Carbon dioxide is a heavier gas than others in the atmosphere, so that it would be expected to sink in enclosed spaces where it is generated by living or dead animals or plants. Day (1938) shows somewhat higher concentrations of carbon dioxide in mounds of *Nasutitermes exitiosus* in Australia than those recorded in Table II. He also states that the normal environment of termites contains high carbon dioxide concentrations to which the termites are tolerant. Holdaway and Gay (1948) interpret the opening of small circular holes by the termites in nests of *Nasutitermes exitiosus* to have the function of reducing carbon dioxide rather than temperature. Day (1938) experimentally demonstrated that *N. exitiosus* does not require carbon dioxide. Cook (1932) showed that *Zootermopsis nevadensis* (Hagen) could tolerate 20% CO_2 concentration and respire normally, but anesthesia occurred in higher concentrations. Cook concludes that respiration of *Zootermopsis nevadensis* remains very near normal in oxygen tensions above five per cent, and there is a well-developed capacity for utilizing extremely small quantities of oxygen. These termites endure quantities of carbon dioxide seldom met in their natural environment, but extreme conditions might occur in wet soils frequented by other species and genera. Day (1938) showed that carbon dioxide concentration reached an equilibrium value that varied in proportion to the size of the ventilation hole in the lid of the container. The author observed a laboratory colony of *Zootermopsis angusticollis* (Hagen) in a two quart Mason jar with a metal lid without a rubber seal. Four separate holes were punched in the lid for ventilation, but the working nymphs plugged these holes with excrement so that the only ventilation was through the plugged holes and around the edge of the metal lid. These termites also built large partitions with particles of excrement that effectively enclosed the inhabited portions of the jar. The ventilation factors in this case may have been oxygen, carbon dioxide, or humidity, or a combination of these. Williams (1934) found an expected inactivation of termites in experimentally high concentrations of carbon dioxide, but he also found a difference in the resistance of *Reticulitermes tibialis* Banks as compared to *R. hesperus* Banks. The former species inhabits drier soils and showed greater sensitivity to carbon dioxide concentrations than did *R. hesperus* which inhabits moister soils with a greater concentration of carbon dioxide. These data suggest that carbon dioxide concentrations in soils or nests may be an important ecological factor and that some physiological tolerance may have evolved in some species, but the data do not indicate that termites react to carbon dioxide specifically nor that there is a homeostasis of this gas in the nest atmosphere.

Nest structures that suggest a ventilation function are the "chimneys" of the mound nests of *Macrotermes* and other fungus-growing genera (Grassé and Noirot 1950, pp. 121, 127, figs. II, V), and the remarkable porous walls of the subterranean nests of *Apicotermes* (Desneux 1948, 1953; Schmidt 1955a). The nests of *Apicotermes* present a phylogenetic sequence of nest structures that strongly indicates the adaptive evolution of behavior patterns that control ventilation. Humidity and temperature do not seem to be regulated by the porous walls of these nests, but fluid water and carbon dioxide might be controlled.

It is difficult to draw positive conclusions from the meager data now available on carbon dioxide concentrations in termite nests. Although termites may tolerate high concentrations, this does not mean that optimal concentrations are high. Oxygen may be a factor also, and may decrease with an increase in carbon dioxide under natural conditions. The ability of the termites to sense carbon dioxide concentrations and to react to them by orientation or nest construction has not been demonstrated. It remains an open question whether the nests are adapted to the regulation of carbon dioxide concentrations, but there is some evidence that suggests that mounds and vertical stratification in soils and on the surface may be differential responses to carbon dioxide concentrations by different species. Whether ventilation mechanisms are adapted to variations in oxygen, carbon dioxide, or humidity, or some combination of these gases, has not been analyzed adequately. All one can be sure of is that the gaseous atmosphere of the nest is homeostatically regulated to some extent.

The exact mechanisms of behavior during the construction of termite nests are very inadequately known and descriptions in psychological terms would still leave us ignorant of the physiological basis in the nervous system and the correlated genetic influences. We know that termites must react to such factors as gravity, space size, space shape, consistency of wood and soil, substrate vibrations, temperature, humidity, and gaseous consistency (Emerson 1938). Their building behavior in the vicinity of a queen is different from that at some distance from the queen. A gradient in the thickness of the cell walls and the organic constituents is detected in some species correlated with distance from the queen (Holdaway 1933; Emerson 1938; Grassé 1939; Grassé and Joly 1941). Biochemical agents seem to control aspects of their social behavior toward themselves and their termitophiles. But their sensory equipment and orientation responses are obviously far more complex and subtle than any that have been precisely observed or experimentally demonstrated. By elimination, we may make some sophisticated guesses concerning their sensory equipment. For example, the regeneration of rain-shedding ridges by blind workers outside and above the nest structure of *Constrictotermes cavifrons* enables us to eliminate some immediate sensory stimuli (Hingston 1932; Emerson 1938). In spite of the dearth of analytical study, however, the geometry, symmetry, replication of structures, and adaptive functions indicate behavioral processes genetically determined, phylogenetically evolved, and ecologically influenced that are both astonishing and challenging. The homeostatic regulation of both physical and biotic factors within the nest has evolved for millions of years and is closely associated with the reciprocal evolution of the social system and the interspecies biocoenosis. Not only is the individual organism a unit in evolution, but the intraspecies supraorganism, the interspecies biocoenosis, and the ecosystem are evolutionary entities that have developed homeostasis.

Summary

Aspects of termite behavior are discussed and illustrated including instinctive social behavior, regeneration of nest structures, responses to humidity, ventilation mechanisms, and the homeostasis of nests.

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ADRENAL AND REPRODUCTIVE RESPONSES TO POPULATION SIZE IN MICE FROM FREELY GROWING POPULATIONS[1]

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INTRODUCTION

The present experiments with growing populations of house mice were designed to explore a mechanism by which environmental factors might operate to limit population growth. Recent studies have shown that there is a common denominator producing the cessation of growth in populations of house mice irrespective of the immediate causal limiting factor: young mice failed to reach adult populations whether the limiting factor was food (Strecker and Emlen 1953), increasing disturbance to parturient mothers (Brown 1953), or remained undetermined (Strecker and Emlen 1953). The failure of young mice to reach the adult population resulted either from a total absence of reproductive activity or a failure of those born to be weaned successfully. Retzlaff (1938) indicated that reproductive failure was a function of population density in experiments with albino mice. He suggested that these density effects were related to behavioral patterns and social structure. The above studies make it appear likely that factors producing a cessation in population growth operate through a common physiological mechanism in conjunction with undetermined socio-psychological factors. It was suggested earlier that there was a density-dependent degree of stress in populations that produced a proportional degree of activity of the pituitary-adrenal axis and suppression of reproduction (Christian 1950). Consequently every population would have an intrinsic upper asymptote to population growth determined by the degree of stress in the population. External environmental limiting factors would act only as additional stressing agents serving to lower the intrinsic upper asymptote. Recent studies with albino and wild house mice in populations of fixed size support this belief (Christian 1955a, 1955b).

Male mice kept in populations of fixed size for one week show changes in organ weight which are related to the population size, and probably also to the prevailing social structure (Christian 1955 a, b). With increasing population size and intact structure their adrenal weights increased, but when the population size exceeded a certain point, their adrenal weights reverted toward lower values, possibly as a result of deterioration of the social structure. On the other hand, the weights of the testes and gonad-dependent organs were inversely related to population size throughout the range studied, and thymus weights varied irregularly. These changes were considered non-specific and typical of responses to the wide variety of stressors described by Selye (1946), the "stress" in point arising from population pressures

[1] The opinions or assertions contained herein are the private ones of the writer and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

which are not precisely definable at present. Since the conditions of the experiments described were highly restricted—animals of one sex being caged together in arbitrarily chosen numbers and compared with completely isolated animals—it remained to be seen whether similar changes would occur as a function of population size in freely growing colonies of mice, containing both sexes. The present experiments were planned to answer this question.

Methods

The procedure followed was similar for each of the following experiments. Laboratory-raised descendants of wild house mice (*Mus musculus*) were used. The young from one or two litters were divided into pairs with one male and one female per pair. One half of the pairs were introduced into a large cage to serve as the starting nucleus of an experimental population. The other half was used to establish a control colony of isolated pairs of mice. Both groups of mice were allowed to breed at will. The litters in the control group were divided and isolated as pairs at weaning, while those in the large cage were left undisturbed. The experimental populations were allowed to grow to a desired size, at which point all of the control and experimental mice were sacrificed. Six experimental populations were used: Four high (1, 2, 3, 6) and two intermediate (4, 5) in size. Control and experimental mice of the second experiment were derived from a pregnant female removed from the first high population. Similarly a pregnant female from the third high population was used to establish the control and experimental colonies of experiment 6. Mice for experiments 3, 4, and 5 were descendants of a pregnant control mouse from the second experiment.

Periodic counts of the young and free-roaming mice were made, and the data plotted against time. The progress of growth of each population was followed in this manner. The "high" populations were sacrificed when their growth curves appeared to be approaching asymptotic values. Populations of intermediate size were sacrificed when they reached a size estimated to be half that of their corresponding high population.

Censuses were infrequent for the first experiment, about every ten days for the second, and at least once a week for subsequent experiments. The census frequency increased as it became apparent that counting did not interfere with the experiments.

The large cages for the experimental populations were 29 x 74 x 42 inches with two decks 21 inches apart. The sides were screened with hardware cloth. A one inch space between the hardware cloth and three sides of the upper deck provided access between the two decks. Twelve one-pound coffee cans with one-inch entrance holes provided nest space. There were four sources of water on each deck. Food in excess, shredded paper nesting material, and sawdust were spread over each deck. All cans appeared to be used equally, and there was no apparent discrimination between the two levels of the cages. The cages were kept in the same room except for the first experiment. Temperature was maintained between 72 and 78° F.

The control and experimental mice were killed with chloroform at the end of each experiment and placed in 10% neutral formalin. Their subsequent treatment was described elsewhere (Christian 1955a). The fixed weights of the adrenal and thymus glands were obtained for every mouse. The weights of the paired preputial glands were obtained for the males from experiments 3, 4, 5, and 6, and for the females from experiments 3, 4, and 5. The lengths of the seminal vesicles and testes were measured for experiments 2 through 6, and the weights of these organs were obtained for experiment 6. The condition of the uterus, the presence or absence of implantation scars, and the number of embryos alive or resorbing were noted for each female from populations 1 through 5.

In the first five experiments the adrenals of both sexes were serially sectioned at 5-7 micra. The widths of the cortical zones were measured as described earlier (Christian 1955a). Cell counts were made on single vertical columns of the fasciculata and X-zones (Zwemer 1936). The testes were sectioned, and the diameters of at least six seminiferous tubules in a central section of each testis were measured with an ocular micrometer. All microscopic measurements are presented in terms of ocular micrometer units. The most advanced stage of spermatogenesis was also determined for the central section of each testis and coded as follows: 1, spermatogonia; 2, secondary spermatocytes; 3, spermatids; 4, a few spermatozoa; and 5, abundant spermatozoa. Sample sections were cut from the other viscera of each mouse and examined for evidence of an active pathological process. None was found.

The cage mean value for each measurement was the unit of experimental comparison, since the mice in any given population could not be considered as independent variates. Each value for one control mouse served as an independent cage mean. A detailed statistical analysis of the rela-

tionship between population size and organ size could not be made because of the small number of experimental populations, each representing a single value. Throughout these experiments the individual results have been grouped into three-gram intervals of body weight. This interval was found to be the smallest convenient for handling the data with an adequate number of mice in each group. Division of the data into body-weight groups was necessitated by the wide range of sizes in each population.

Results

I. *Population development*

The growth of each population is summarized graphically (Figs. 1-4). Experiment one is not shown as there were insufficient counts. The population in experiment 1 reached a maximum size of 21 free-roaming mice within 45 days after intial introduction. All subsequent litters failed to survive, and adult mortality reduced the population to 18 at 93 days, when it was sacrificed. In subsequent discussions the results from experiment 1 have been combined with those from experiment 2, as the adrenal weights of the 10 male and 8 female mice from experiment 1 were the same as those for corresponding body weights from experiment 2 ($P > 0.40$).

The form of the growth curve was essentially similar for all populations, and appeared to be sigmoid. The birth-rate and the proportion of young born which survived to reach the free-roaming population declined steadily with increasing population size (Fig. 5). The increases in infant mortality occurred primarily in those over four days old. They usually died in about ten days to two weeks after birth, and were found uninjured, and usually with empty stomachs. There was a steady decrease in the number of young reaching the free-roaming population in the upper half of the high population growth curves, because of the declining birth and infant survival rates. The data indicated that the three high populations were approaching their maximal size (Fig. 5). The data from the intermediate populations were inadequate for such a detailed analysis, but they appeared to follow the same pattern.

There were successive increases in maximal population size in experiments 1, 2, 3, and 6, each population being larger than the one before.

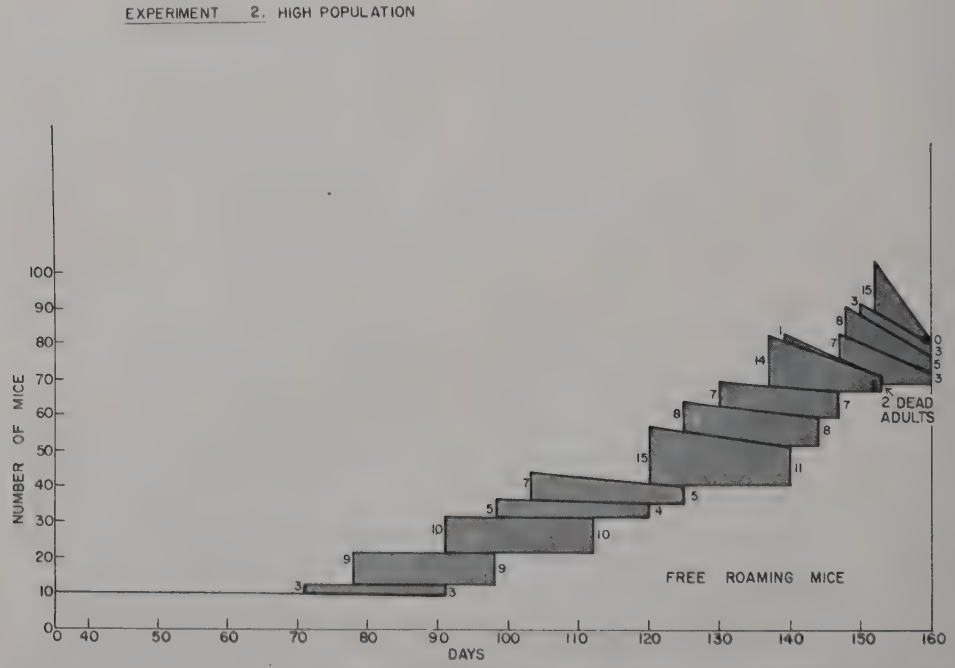

Fig. 1. Growth of the high population of wild house mice from experiment 2. Left hand vertical lines represent the number of young born; right hand the number of young reaching the free roaming population. Shaded areas represent the nestling young.

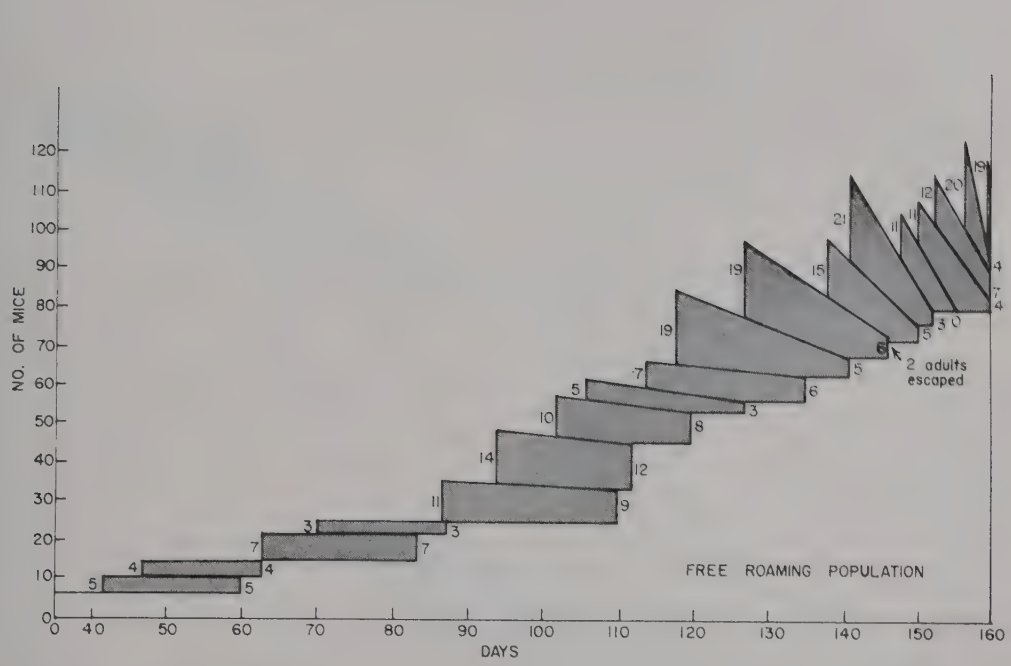

FIG. 2. Growth of the high population of wild house mice from experiment 3. For explanation of the graph see Fig. 1.

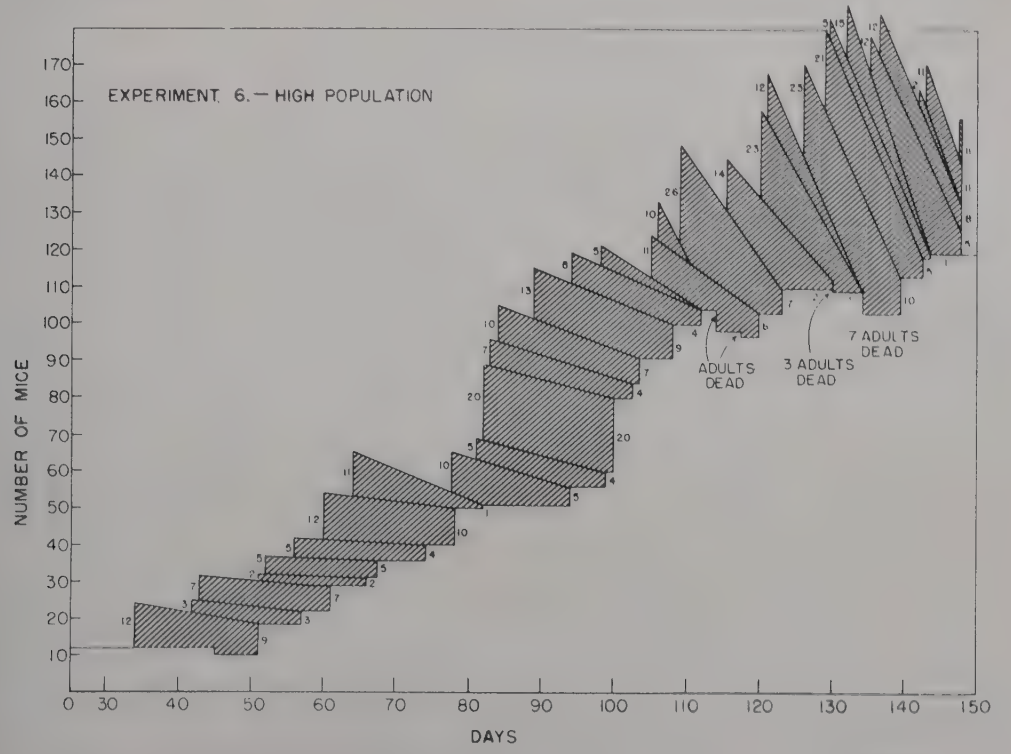

FIG. 3. Growth of the high population of wild house mice from experiment 6. For explanation of the graph see Fig.1.

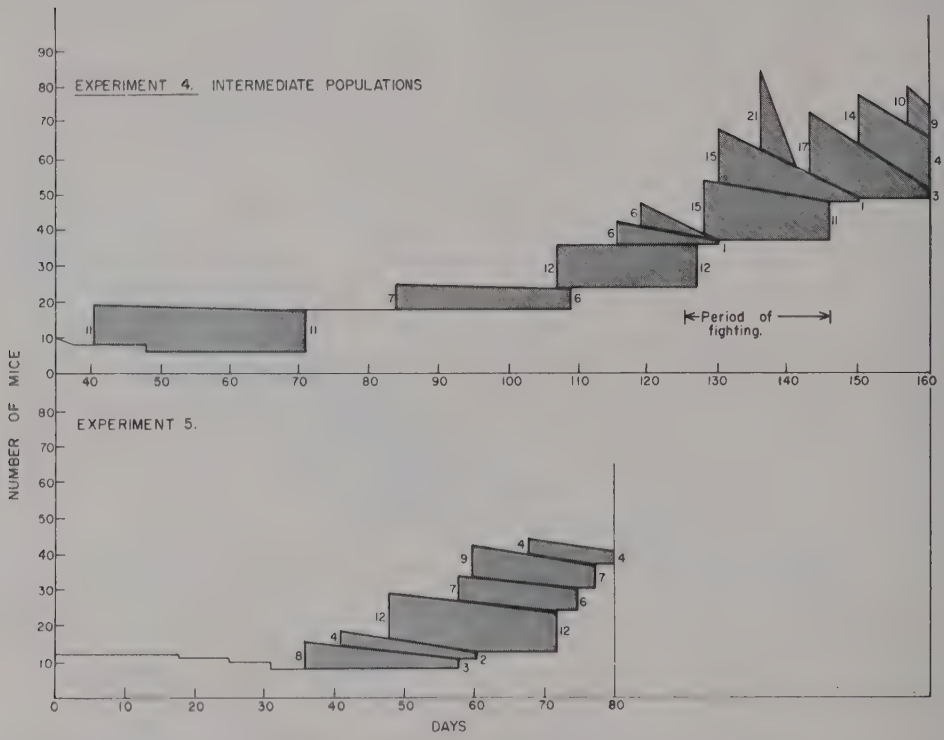

FIG. 4. Growth of the intermediate populations of wild house mice from experiments 4 and 5. For explanation of the graphs see Fig. 1.

II. *Organ measurements: male mice*

Adrenal glands. The adrenal weights of the male mice from high populations (1, 2, 3, 6) were consistently heavier than their controls except in the lowest body weight groups, where there was some convergence (Table I; Fig. 6). The averages of the weight-group mean adrenal weights for the high populations (1, 2, 3, 6) were 6.10, 5.71, and 5.14 milligrams, and their control weights were 4.71, 4.42, and 4.31 milligrams, representing increases of 28, 28, and 19% respectively in mean adrenal weight. Note that there was a gradual decline in adrenal weight in the control and experimental males with successive experiments.

The mean adrenal weights of male mice from the intermediate populations (4, 5) increased 9 and 15% respectively over their controls (Table I). The results from populations 4 and 5 were combined for convenience, as they both had the same controls in common with high population 3.

There was a distinct break in the adrenal weight curve with respect to body weight for the high populations. The adrenal weight increased rapidly with body weight to the 16-18.9 gram body weight group, then levelled off. The curve for the control adrenal weights was somewhat similar, but the change in slope was less acute and the gain in weight was slower in the lower half of the curve (Fig. 6). The adrenal weight curve for the intermediate populations was between the control and high population curves.

Changes in adrenal weight of the larger mice paralleled changes in the width of the zona fasciculata. There were mean increases in fasciculata width of 35% in the high, and 16% in the intermediate populations (Fig. 7), when the results from experiments 1, 2, and 3 were combined in one group and from experiments 4 and 5 in another. Differences in fasciculata width did not account entirely for the differences in weight between the control and experimental adrenals in the lower half of the body weight range, even though the fasciculata was wider than its control counterpart throughout the entire body weight range. The more rapid increase in adrenal weight with respect to body weight in the smaller experimental mice was a result of a wider X-zone than in the control mice (Fig. 7).

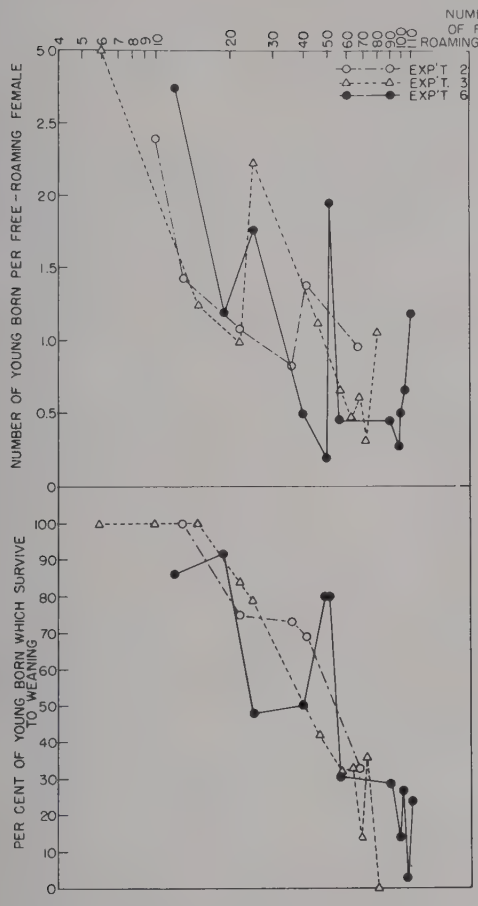
NUMBER OF FREE-ROAMING MICE
EXP'T 2
EXP'T 3
EXP'T 6
NUMBER OF YOUNG BORN PER FREE-ROAMING FEMALE
PER CENT OF YOUNG BORN WHICH SURVIVE TO WEANING

FIG. 5. Birth-rates (top) and survival rates to weaning (bottom) of infant mice plotted against population size for experimental populations 2, 3, and 6. The rates in each case were calculated for each change in the number of free-roaming mice in the population. Note that as the size of the population increases the survival rate of the young decreases markedly, although there is a low death-rate among the adults.

Increases in the number of cells in vertical columns of the fasciculata and X-zones paralleled increases in zonal widths. The fascicular cells of mice from the high populations averaged 1.08 ocular micrometer units in diameter compared to 0.91 units in their controls. Cellular hyperplasia and hypertrophy produced the increased width of the zona fasciculata in the experimental mice.

Thymus gland. The thymus weights from the three high populations were heavier than their controls in mice weighing less than 19 grams (Table I; Fig. 6). Above that body weight the experimental thymus glands declined rapidly in weight, and were well below their control values in mice weighing 25 or more grams. The weight of the thymus glands remained relatively constant for all body weights of the control mice. The pattern of weight change of the thymus glands from the intermediate populations was similar to that for the high populations except for greater weights in the lower end of the body weight range. The control and experimental thymus weights from experiment 6 were lower than those for earlier experiments.

Preputial glands. There was a delayed onset of rapid increase in preputial gland weight with respect to body weight in high populations 3 and 6 and intermediate populations 4 and 5 compared to their controls (Table I). The preputial glands of the experimental mice began increasing rapidly in weight at a body weight three grams heavier than in the control mice. However, once they began to gain weight rapidly, they continued to gain through the heavier body weight groups, whereas the preputial glands of the control mice stopped gaining weight at 25-27.9 grams of body weight (Fig. 6). There was an earlier increase in preputial weight with respect to body weight in the control and experimental mice from experiment 6 than for the preceding experiments.

Seminal vesicles. The mean seminal vesicle lengths for experiments 2 through 6 when plotted against their respective body weight groups produced sigmoid curves with an initially slow rate of increase in length followed by a period of rapid lengthening, and finally a return to a slow rate of increase (Table I; Fig. 6). Rapid lengthening of the seminal vesicles began at a body weight of 10-12.9 grams in the control mice and 13-15.9 grams in the mice from high populations, but once begun their rate of increase was similar in both groups. The curve for the mean seminal vesicle length with respect to body weight for the intermediate populations was irregular; but by and large it was between the curves for the control and high populations, possibly closer to the latter. Rapid growth of the seminal vesicles from experiment 6 began at a somewhat lower body weight than in the other experiments.

The changes in weight of the seminal vesicles in experiment 6 paralleled the changes in length for the same population (Table I; Fig. 6). The seminal vesicles from the high population mice were lighter than their controls for all body weights. The organ weights were probably more accurate than the linear measurements and confirmed the changes determined by the latter.

Testes. Testicular development with respect to body weight was more advanced in the controls than in the mice from high populations (Table I;

TABLE I. Organ weight and length data collected from male mice from freely growing populations and their controls. The data are given as the mean for each 3 gram body weight interval with the number of mice in parentheses

		Grams, Body Weight								Mean of Weight group Means
		7-9.9	10-12.9	13-15.9	16-18.9	19-21.9	22-24.9	25-27.9	28+	
Mean Paired Adrenal Wt. per Body Weight Group *Mg. with No. animals in parens.* — Intermediate High Populations	Controls 1 & 2..	3.02(4)	4.41(6)	4.63(2)	4.70(5)	5.68(7)	4.94(9)	4.74(7)	5.54(1)	4.71
	" 3, 4, 5..	3.03(4)	3.34(6)	3.90(4)	5.13(5)	5.31(2)	4.71(13)	4.93(15)	5.03(3)	4.42
	" 6.....	2.71(1)	3.91(4)	3.81(3)	4.30(15)	4.74(12)	4.44(6)	4.73(4)	5.86(4)	4.31
	Expt'l. 1 & 2....	3.65(2)	—	6.13(9)	6.45(9)	6.66(10)	6.44(5)	6.27(3)	7.10(9)	6.10
	% chge. from Controls.....	+21%		+32%	+37%	+17%	+30%	+32%	+28%	+28%
	Expt'l. 3.....	3.00(3)	3.42(1)	5.56(3)	6.60(7)	6.18(9)	6.11(5)	6.28(5)	7.62(5)	5.71
	% chge. from Controls.....	−1%	+29%	+43%	+29%	+16%	+30%	+28%	+52%	+28%
	Expt'l. 6.....	2.65(7)	3.15(3)	4.56(7)	5.20(12)	5.50(13)	6.41(12)	6.23(7)	7.44(7)	5.14
	% chge. from Controls.....	−2%	−19%	+20%	+21%	+16%	+44%	+32%	+27%	+19%
	Expt'l. 4.....	2.12(1)	—	—	5.59(8)	6.69(3)	5.22(4)	5.43(5)	6.46(6)	5.25
	% chge. from Controls.....	−30%			+9%	+26%	+11%	+10%	+28%	+ 9%
	Expt'l. 5.....	2.48(6)	3.93(5)	4.79(1)	4.41(1)	—	—	6.87(1)	6.99(1)	4.91
	% chge. from Controls.....	−18%	+18%	+23%	−14%			+39%	+39%	+15%
Mean Thymus Wt. per Body Wt. Group mg.	Controls 1, 2....	58	56	39	59	35	30	48	44	46.1
	" 3, 4, 5..	57	72	60	70	84	56	51	50	62.5
	" 6.....	49	36	30	32	34	35	41	30	35.9
	Expt'l. 1, 2....	63	56	62	53	34	42	18	18	43.3
	" 3.....	73	—	80	61	38	24	45	21	42.8
	" 6.....	46	50	52	48	32	42	23	22	39.4
	" 4.....	71	—	—	73	79	40	27	20	61.9
	" 5.....	57	80	100	117	—	—	55	69	
Mean Paired Preputial Gland Wt. per Body Wt. Group Mg.	Controls 3, 4, 5..	4.5	5.5	12.6	27.5	63.5	79.7	90.2	88.3	48.5
	" 6.....	12.2	12.5	32.4	53.7	54.5	67.5	70.7	64.4	46.0
	Expt'l. 3.....	6.0	—	9.5	16.4	24.5	50.8	65.4	142.0	39.3
	" 6.....	7.7	16.8	8.3	27.6	37.1	39.6	86.1	131.0	44.3
	" 4.....	4.6	—	—	22.8	21.6	50.4	91.4	145.3	41.9
	" 5.....	3.6	8.6	10.2	13.8	—	—	48.6	68.2	
Mean Seminal Vesicle Length, mm. per Body Weight Group	Controls 2.....	2.4	3.3	7.0	8.0	9.5	12.8	12.5	13.0	8.6
	" 3.....	3.3	3.6	5.5	8.6	11.5	14.5	16.7	18.7	10.3
	" 6.....	6.0	6.8	11.7	15.5	17.4	20.3	20.3	20.8	14.9
	Expt'l. 2.....	2.3	3.0	2.9	5.3	5.9	12.0	15.0	14.3	7.6
	" 3.....	2.5	—	3.2	5.1	9.0	12.2	12.2	15.6	8.9
	" 6.....	3.0	6.3	4.0	8.2	12.8	13.5	18.6	21.1	10.9
	" 4.....	3.5	—	—	6.1	5.0	13.3	14.8	18.3	9.4
	" 5.....	4.9	5.6	6.0	6.0	—	—	14.0	26.0	
Mean Sem. Ves. Paired Wt. per Body Wt. Grp.	Controls 6.....	6.4	10.4	35.9	69.8	99.0	128.2	161.7	204.7	
	Expt'l. 6.....	3.8	9.7	6.6	16.4	40.0	56.2	128.0	142.7	
Mean Testis Length per Body Wt. Group mm.	Controls 2.....	4.38	6.08	7.50	6.90	8.17	7.94	8.19	—	7.02
	" 3, 4, 5..	4.13	5.25	5.88	7.10	8.25	7.85	8.22	8.67	6.92
	" 6.....	6.00	6.50	6.25	6.80	7.64	7.50	8.25	7.50	7.06
	Expt'l. 2.....	4.00	—	4.54	6.17	7.39	7.90	8.00	7.94	6.56
	" 3.....	3.00	—	3.83	5.50	6.56	7.30	6.50	7.88	5.07
	" 6.....	3.57	4.67	4.49	5.67	7.08	7.08	7.57	8.14	6.03
	" 4.....	4.00	—	—	5.28	5.67	6.50	7.00	8.25	5.94
	" 5.....	4.08	4.80	6.00	6.00	—	—	6.00	8.50	
Mean Paired Testis Wt. per Body Wt. Grp. Mg.	Controls 6.....	75.6	88.7	112.6	143.1	171.1	178.3	209.3	174.5	
	Expt'l. 6.....	20.7	60.3	34.1	84.5	132.3	141.2	170.4	180.5	

TABLE I. (Continued)

		Grams, Body Weight								Mean of Weight group Means
		7-9.9	10-12.9	13-15.9	16-18.9	19-21.9	22-24.9	25-27.9	28+	
Mean Seminiferous Tubule Diam. per Body Wt. Group No. *Mice in Paren. for ea. Popn. Class*	Controls									
	2, 3, 4, 5.....	9.9(8)	13.9(12)	17.3(4)	17.0(9)	20.6(8)	19.9(18)	19.4(17)	20.4(4)	17.3
	Expt'l. 2, 3....	10.0(5)	8.3(1)	10.3(7)	13.9(12)	18.2(18)	18.5(8)	17.6(5)	19.9(12)	14.6
	Expt'l. 4, 5....	11.1(7)	12.7(5)	17.0(1)	15.5(7)	16.3(3)	16.3(3)	19.2(6)	Not Meas.	15.3
Mean Spermatogenesis values per Body Wt. Group *Results Comb.*	Controls									
	2, 3, 4, 5.....	1.40	3.08	4.00	4.30	4.94	4.83	4.94	5.00	3.93
	Expt'l. 2, 3....	1.50	2.00	2.10	4.16	4.50	4.70	4.90	5.00	3.41
	" 4, 5....	1.86	3.00	3.00	3.43	3.00	4.50	4.67	Not Meas.	3.75

Fig. 6). The curves for testis length paralleled those for preputial gland weight and seminal vesicle length. The lengths of the testes form the intermediate populations varied, but approximated those for the high populations. The control testes in the lower body weight groups of experiment 6 were larger than those for the earlier experiments.

The curves for the weights and lengths of the control and experimental testes from experiment 6 paralleled each other (Fig. 6), and demonstrated a delay in development similar to the other high population mice.

The curves for the diameters of the control and experimental seminiferous tubules from experiments 2, 3,3, 4, and 5 parallel their corresponding curves for testicular length. The curves for the advancement of spermatogenesis with respect to body weight similarly paralleled those for testicular length. The tubules of control mice were wider and enlarged at a lower body weight than in the experimental mice. Spermatogenesis similarly proceeded more rapidly with respect to body weight in the control mice than in those from high populations. The values for the intermediate populations were closer to those for the high populations than for the controls.

III. *Organ measurements: female mice*

Adrenal glands. In every high population (1, 2, 3, 6) there was a rapid increase in adrenal weight with respect to body weight until a body weight of 19-21.9 grams was reached (Table II; Fig. 8). Adrenal weight was relatively constant in female mice weighing over 19 grams. Below a body weight of 15.9 grams the adrenal weights of the control and experimental females were similar. Above 16 grams of body weight the averages of the weight group means of female adrenals from the high populations were 9, 20, and 13% heavier than their respective controls, and those from the intermediate populations were 3 and 5% heavier than their controls. However, the mean adrenal weights for all body weights of the high populations were —3, +23, and +1% greater than their respective controls.

The widths of the zona fasciculata for experiments 1 through 3 combined were greater than their combined controls for every body weight interval, but especially in females weighing more than 16 grams (Fig. 9). The widths of the zona fasciculata of mice from the intermediate populations were similar to their controls. The width of the X-zone was essentially the same in both control and experimental females weighing under 16 grams and over 25 grams (Fig. 9). Involution of the X-zone was delayed with respect to body weight in female mice from the intermediate and high populations, as the X-zone of females weighing between 16 and 25 grams was wider in the high populations than in the controls. The widths of the X-zone in the intermediate populations were similar to those from the high populations except for females weighing 22-24.9 grams, which had wider X-zones than either the control or high population females of the same body weight.

There were more cells in vertical cords of the zona fasciculata of mice from the high populations

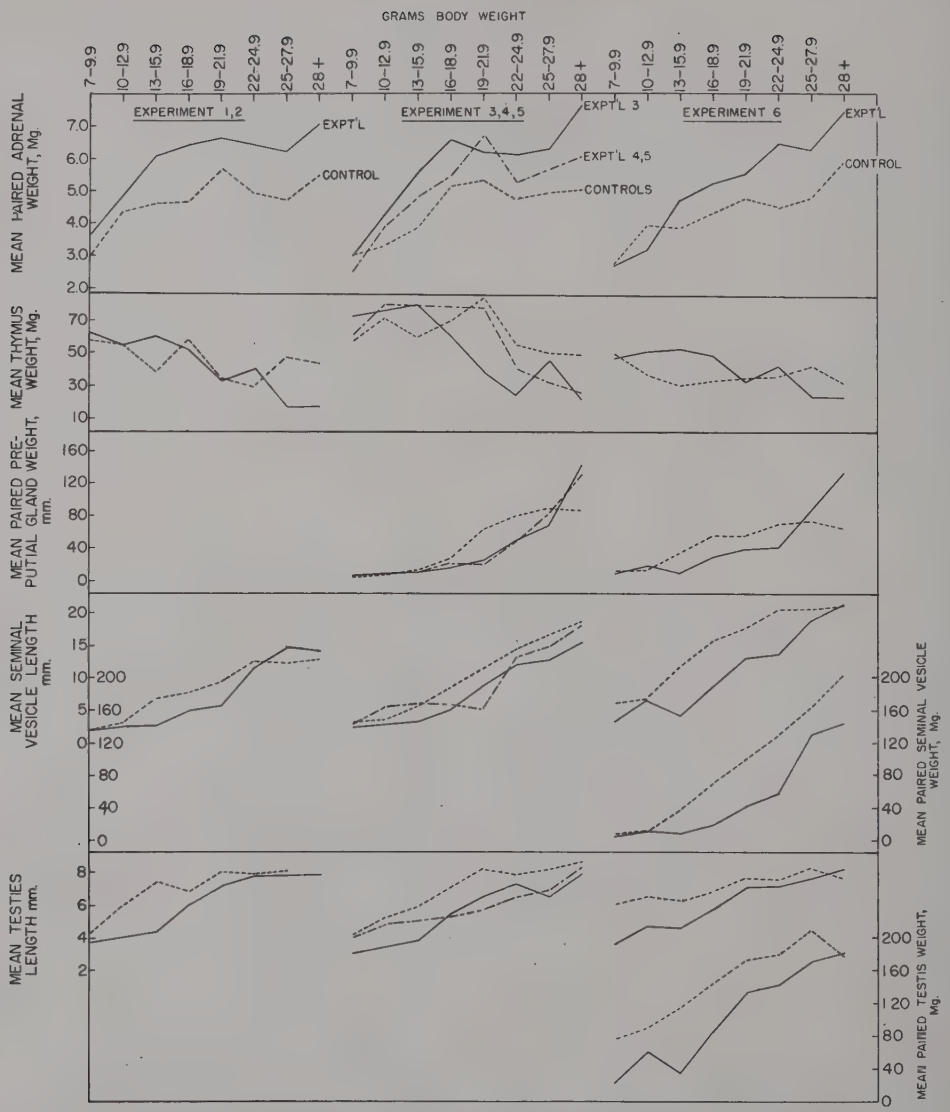

FIG. 6. Organ weight and length data from male mice plotted as the mean for each 3-gram body weight interval.

than in the controls except in the heaviest body weight interval (Fig. 9). Curves for the number of cells in cords of the X-zone with respect to body weight paralleled those for the widths of this zone. Adrenal weight is affected more profoundly by changes in the width of the fasciculata than by equal changes in the width of the X-zone, as the fasciculata is peripheral to the X-zone.

The adrenal weight of the control and experimental female mice declined with successive experiments, paralleling a similar decline in adrenal weight in the male mice.

Thymus gland. Little would be gained by a detained discussion of the female thymus gland weights (Table II; Fig. 8). Thymus weight declined gradually with increasing body weight, but there was no consistent change with population size.

Preputial glands. The preputial gland weights of female mice from high population 3 were greater

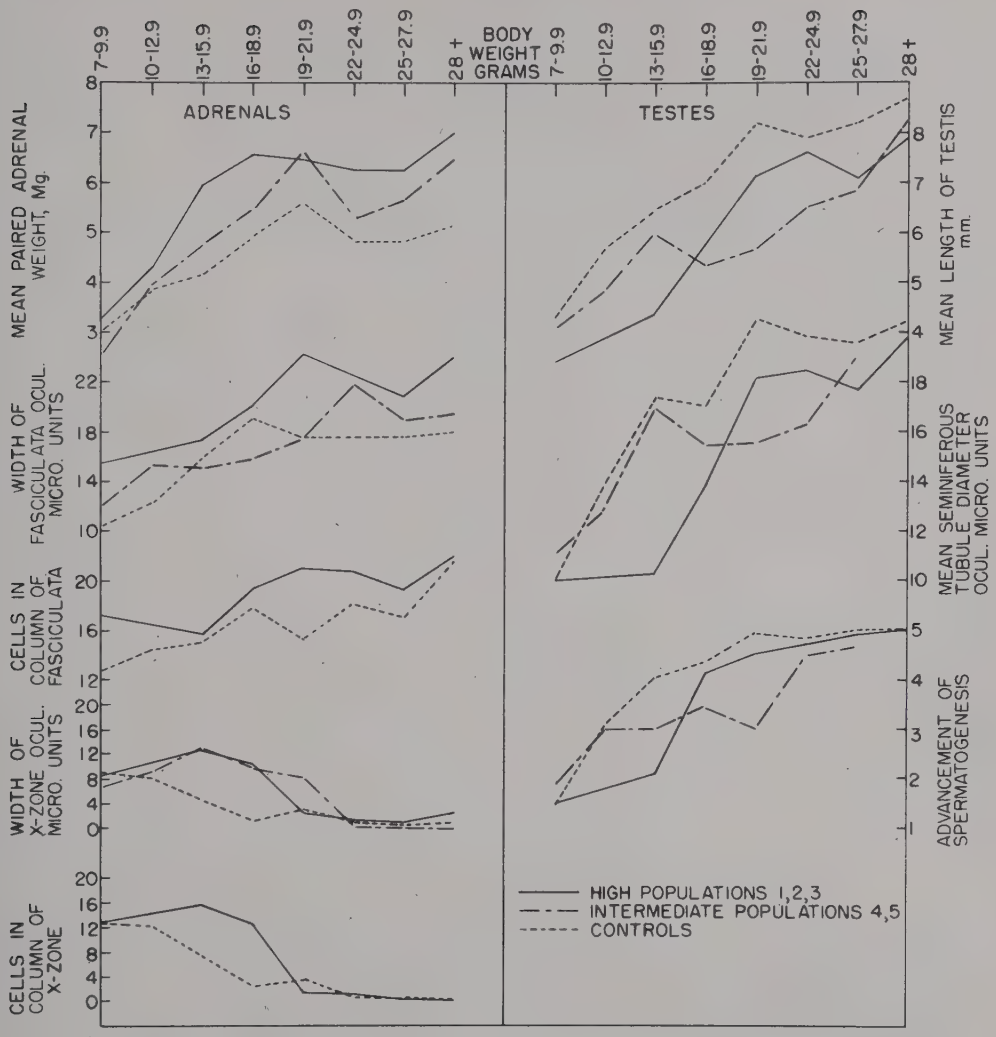

FIG. 7. Microscopic measurements of the adrenals and testes of male mice plotted as the means for each 3-gram interval of body weight. Microscopic measurements were obtained for the following numbers of mice for each body weight group respectively from the lightest through the heaviest: 4, 0, 6, 12, 18, 10, 6 and 13 from the high populations; 7, 4, 1, 9, 3, 3, 5 and 7 from the intermediate populations; and 6, 9, 5, 7, 7, 19, 19 and 3 from the control mice.

than their controls (Table II; Fig. 8). Those for intermediate populations 4 and 5 were between the control and high population values, but closer to the latter. The female preputial glands from the experimental populations began increasing rapidly in weight at a lower body weight (19-21.9 grams) than in the control mice (22-24.9 grams).

Reproduction. The data collected at autopsy on the productivity per female for populations 1 through 5 were combined and compared with the control values similarly combined (Table III), as they were inadequate for inter-experiment comparison. The number of females with resorbing embryos and the mean number of visibly resorbing embryos per pregnant female were greater in the experimental populations than in the isolated controls. The proportion of females with enlarged uteri which were pregnant, the number of grossly viable embryos per pregnancy, the mean total litter size per pregnancy, the mean number of normal embryos per female with enlarged uteri, and the number of apparently normal embryos per female weighing 20 or more grams were all lower values in the experimental mice than in the controls. The

TABLE II. Organ weight data collected from female mice from freely growing population and their controls. The data are given as the mean for each —3 gram body weight interval with the number of mice in parentheses

		Body Weight, Grams									Means of weight group means	Means of group means 16 gms.
		7-9.9	10-12.9	13-15.9	16-18.9	19-21.9	22-24.9	25-27.9	28-30.9	31+		
Mean Paired Adrenal Weight per Body Weight, Mg. No. mice in parentheses												
High Populations	Controls 1, 2	3.70(4)	5.24(6)	7.26(5)	7.54(9)	9.19(5)	9.31(5)	11.29(3)	9.90(2)	10.05(2)	8.16	9.55
	" 3, 4, 5	1.97(3)	3.47(9)	5.76(4)	7.28(15)	7.83(6)	8.25(5)	7.06(7)	7.01(5)	9.44(4)	6.45	7.81
	" 6	3.81(6)	5.82(3)	6.65(8)	7.89(14)	7.91(11)	7.12(3)	8.78(6)	6.72(1)	8.35(3)	7.01	7.80
	Expt'l. 1, 2	2.77(2)	4.67(2)	4.06(2)	8.75(9)	10.53(10)	10.20(3)	10.88(1)	10.62(4)	10.84(6)	8.15	10.30
	% change from Controls	−25	−11	−44	+16	+15	+10	−4	+7	+8	−3	+9
	Expt'l. 3	2.85(4)	4.18(2)	—	8.16(11)	10.42(6)	9.37(5)	8.38(6)	9.46(5)	9.96(6)	7.85	9.29
	% change from Controls	+45	+20	—	+12	+33	+14	+19	+35	+5	+23	+20
	Expt'l. 6	2.40(6)	4.43(7)	5.98(2)	8.21(7)	9.09(7)	8.39(9)	9.08(7)	8.66(3)	8.86(13)	7.23	8.71
	% change from Controls	−37	−24	−10	+4	+15	+18	+4	+29	+6	+1	+13
Intermediate Populations	Expt'l. 4	—	5.05(1)	5.24(1)	6.95(4)	8.49(1)	9.37(1)	8.09(4)	7.72(4)	7.32(4)	7.28	7.97
	% change from Controls	—	+45	−9	−4	+8	+14	+14	+10	−22	+7	+3
	Expt'l. 5	2.69(6)	4.23(3)	4.35(2)	7.37(2)	8.41(1)	10.64(2)	—	7.53(2)	7.49(5)	6.59	8.29
	% change from Controls	+37	+22	−25	+1	+7	+29	—	+7	−21	+7	+5
Mean Thymus Weight per Body Weight Group, mg.	Controls 1, 2	51	43	37	44	37	35	23	16	18	33.5	
	Controls 3, 4, 5	51	61	79	61	61	53	63	46	38	56.9	
	Controls 6	37	63	35	43	44	61	41	15	19	39.6	
	Expt'l. 2, 1	47	59	64	51	52	55	60	40	37	51.7	
	Expt'l. 3	44	92	—	56	46	43	43	36	40	49.8	
	Expt'l. 6	45	38	54	57	56	46	33	35	17	42.3	
	Expt'l. 4, 5	65	83	83	83	88	68	58	28	31	65.1	
Mean Paired Preputial Gland Weight, mg.	Controls 3, 4, 5	20	3.5	3.2	5.7	6.6	11.9	18.1	14.2	15.5	8.9	
	Expt'l. 3	4.2	7.5		11.0	17.3	32.5	34.2	50.6	43.0	25.0	
	Expt'l. 4, 5	2.7	5.3	5.6	8.2	6.1	23.8	27.7	32.2	29.2	15.6	

TABLE III. Reproductive data from female mice from the large cage freely growing population, experiments 1 through 5, and their controls

Experiment Number	Number with Enlarged Uteri	% Visibly Pregnant	% Pregn. with Resorbing Embryos	Number Grossly Viable Embryos	Mean Number Viable Embryos Per Pregnancy	Number Visibly Resorbing Embryos	Average Number Visibly Resorbing Per Pregnancy	Mean Total Litter Size Per Pregnancy	Mean Number Normal Embryos Per Mature ♀	Number ♀♀ >20 gms.	Number Normal Embryos ♀ >20 gms.
EXPERIMENTAL FEMALES											
1	4	50	0	13	6.5	0	0	6.50	3.25	4	3.25
2	23	39 (39%)	22	48	5.3	2	0.4	5.56	2.09	16	3.00
3	25	28	43	40	5.7	11	1.6	7.29	1.60	26	1.54
4	13	54 (59%)	57	31	4.6	17	2.4	6.50	2.38	14	2.38
5	11	64	57	36	5.1	7	1.0	6.15	3.27	10	3.60
TOTALS	76	285	179	168	27.2	37.0	5.4	32.00	12.59	70	13.77
Mean	15.2	47.5	35.8	33.6	5.4	5.4	1.08	6.40	2.52	..	2.75
% change from Controls	....	−18%	+91%	....	−13%	....	+59%	−7%	−22%	....	−16%
									COMBINED INDIVIDUAL DATA....		2.40
									% CHANGE FROM CONTROLS....		−31%
CONTROLS											
1	4	75	0	15	5.0	0	0	5.00	3.75	5	3.22
2	10	50	20	29	7.3	3	0.75	8.00	2.90	9	3.00
3	29	48	36	88	6.3	18	1.3	7.60	3.03	24	3.66
TOTALS	43	173	56	132	18.6	21	2.05	20.60	9.68	38	9.88
Mean	14.3	57.7	18.7	44.0	6.20	7.0	0.68	6.87	3.23	..	3.29
									COMBINED INDIVIDUAL DATA....		3.47

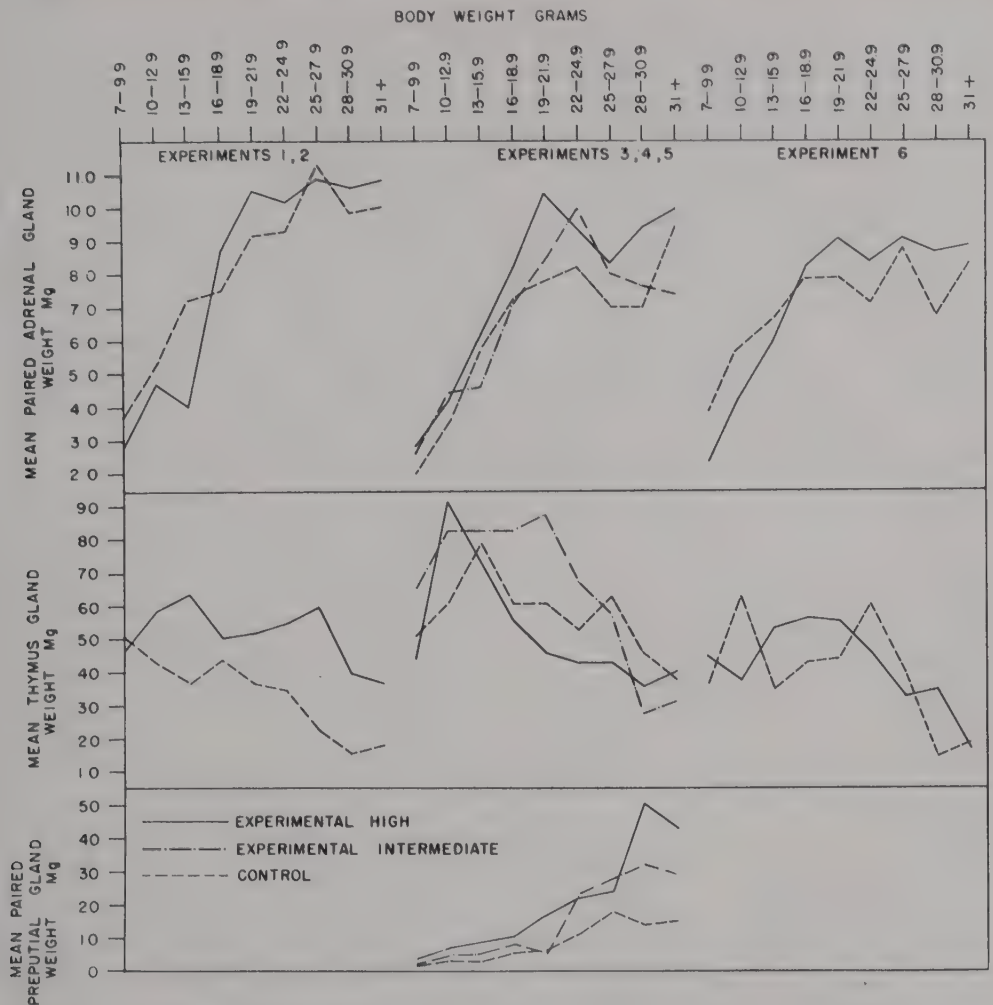

FIG. 8. Organ weight data from female mice plotted as the mean for each 3-gram body weight interval.

20-gram weight was used because no smaller females were found pregnant. There was a 31% decline in the number of normal embryos per mature female in the experimental populations when all experimental mice are considered as one group and all controls another. Errors inherent in obtaining these data tended to minimize the differences between the control and experimental mice. Recently dead embryos may have been called viable, and very early pregnancies in both groups were missed on gross examination. In addition pregnancies were counted at all stages and resorptions tended to increase with respect to the controls as gestation advanced.

The reproductive data collected by autopsying female mice and by counting the living populations were mutually supportive and indicated a decline in the pregnancy rate, total litter size, and survival of young in utero in the mice from the experimental populations.

IV. *Statistical evaluation*

It was pointed out earlier (Christian 1955 a, b) that only the mean value for each measurement from a population may be used to test the relationship between that measurement and population size. The mice in a population are not independent variates, regardless of their numbers, hence the "cage mean value" of each experimental measurement must be used for statistical testing. The number of freely growing populations was too small to test the relationship between population size and organ size. Nevertheless control and experimental individual measurements were com-

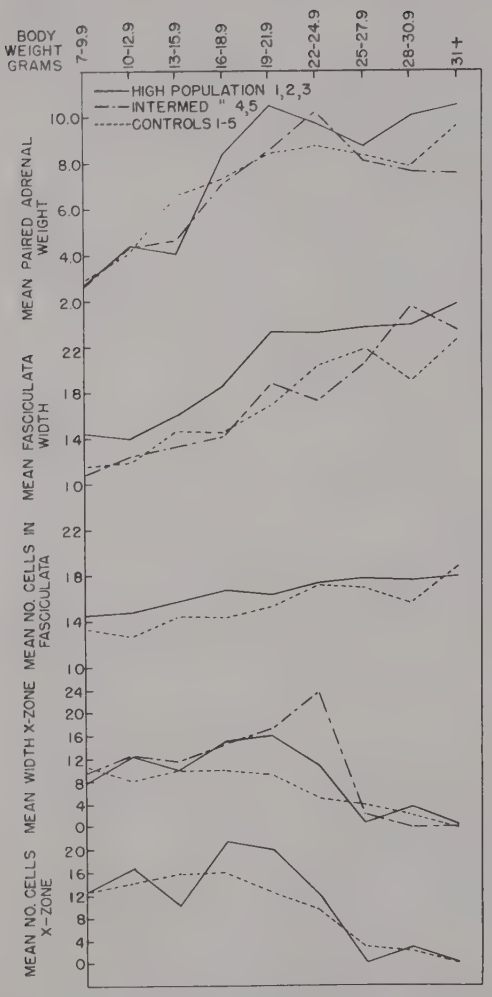

FIG. 9. Microscopic measurements of the adrenal cortices of female mice plotted as the means for each 3-gram interval of body weight. The mean values were derived from measurements of the adrenals for the following numbers of mice for each body weight group respectively: 5, 4, 1, 20, 14, 8, 6, 8 and 11 for the high populations; 5, 4, 3, 5, 2, 2, 4, 6 and 9 for the intermediate populations; and 6, 12, 5, 22, 9, 9, 9, 7 and 5 for the control female mice.

pared by analyses of variance for each high population experiment without basing any conclusions on the significance of their differences. Adrenal and preputial gland weights, testicular length and weight, seminal vesicle length and weight, seminiferous tubule diameter, and width of the zona fasciculata differed significantly ($P < 0.01$ or better) between the control and experimental male mice in every experiment for which the measurements were taken. The same statement of significance is true for the measurements of female mice except in experiment 6 in which the adrenal weights of the experimental mice were significantly greater than the control values only if the three lower weight groups were omitted from consideration. These data show significant differences between the control and experimental values, although the significance cannot be attached to the relationships to population size.

These experiments provide an index of the organ changes taking place in mice or different body weight as well as with population size. Body weight provides a rough indication of age, although in no way can it be construed to be a precise method of determining the age of a mouse.

Discussion

A relationship was demonstrated between adrenal weight and population size in experiments with populations of fixed size. Adrenal weight was related in turn to the amount of adrenocortical tissue, primarily of the zona fasciculata. This zone in mice of both sexes is directly dependent on pituitary adrenocorticotrophin (ACTH) (Jones 1949b), so that increases in adrenal weight were considered attributable to stress in the populations acting via the pituitary. In the present studies the mean adrenal weights of male mice from the freely growing populations were greater than those from their isolated controls. The adrenals from high populations were the heaviest, the controls were lightest, and those from the intermediate populations were intermediate in weight. Increases in adrenal weight in the experimental mice were largely attributable to hyperplasia and hypertrophy of the adrenal cortex, especially of the zona fasciculata.

The cortical X-zone, as well as the zona fasciculata, contributed to the differences in adrenal weight of experimental male mice weighing less than 19 grams. However, this zone had begun to involute in experimental males weighing 16-18.9 grams, indicating that they were reaching sexual maturity. The X-zone was not considered in earlier experiments, as all of the mice were mature males at the time of sacrifice.

The X-zone of the mouse is a transitory zone of the adrenal cortex immediately surrounding the medulla (Howard 1927). It is dependent on pituitary gonadotrophins, probably luteinizing hormone (LH), for its maintenance, and is completely independent of ACTH (Jones 1948, 1949b). The X-zone of male mice is involuted at puberty by the increase in circulating androgens (Howard 1927; Waring 1935). Several authors

have shown that this zone is unaffected by adrenal steroids (McPhail and Read 1942; Antopol 1953; Allen 1954), and that its involution in male mice is specifically an effect of androgens (Jones 1948; 1949a). A decrease in circulating LH at puberty may augment its involution (Jones 1949a). The X-zone is involuted during the first pregnancy (Tamura 1926; Howard 1927; Waring 1935) of female mice by chorionic gonadotrophins (Jones 1948). There was a broad age range in the mice in the present experiments; so that the X-zone of the adrenal cortex became a prominent consideration. Before puberty the adrenal cortex provided a measure of ACTH production, consequently stress, as well as a measure of the sex hormones. After puberty, the cortex measured only stress.

Delayed involution, even growth, of the X-zone with respect to body weight of male mice from the freely growing populations is attributable to a decrease in circulating androgens, and probably to a continuing high level of circulating LH as well.

The decrease in adrenocortical width (zona fasciculata plus X-zone) in male mice weighing more than 19 grams was not reflected in the adrenal weight curves. Failure of the weight to decline could be explained by an increase in medullary width (Bullough 1952). However, such an increase could not make an important contribution to the weight of the gland, because: (1) central location of the medulla would minimize its weight contribution compared to the cortex, and (2) an increase in medullary width with a constant cortical width necessarily would entail an increase in cortical mass, and the width of the zona fasciculata increased regularly with increasing body weight. The medulla probably enlarged to occupy a space approximately equal to that once occupied by the X-zone.

The hormonal controls of the secondary sex organs, testes, and thymus are sufficiently well understood to use their measurements as rough assays of the endogenous production of their controlling hormones. Growth of the preputial glands is stimulated by androgens, and to a lesser extent by ACTH (Jacot and Selye 1951; Hess, Hall, Hall, and Finerty 1952). Their growth is suppressed by estrogens (Selye 1947; Rennels, Hess, and Finerty 1953). Growth of the seminal vesicles is controlled by androgens (Burrows 1949). Spermatogenesis and the size of the testes are controlled mainly by gonadotrophins (Burrows 1949). The diameter of the seminiferous tubules is primarily another measure of spermatogenesis. The data derived from these organs can be used to further interpret and support the adrenal data.

Shifts with respect to body weight in the growth curves of the preputial glands, seminal vesicles, and testes of the experimental mice coincided with the delayed involution of the X-zone in experiments where the measurements were taken. These organs began rapid growth at a greater body weight, and presumably age, than in the control mice, indicating a suppression of androgens and gonadotrophins (probably FSH) with a delay in the onset of puberty. The adrenal X-zones were not measured for experiment 6, but the measurements of the reproductive organs suggest that there was an earlier production of androgens in the experimental and control male mice than in the preceding experiments. Therefore, earlier involution of the X-zone probably accounted for the more gradual increases in adrenal weight with respect to body weight in this experiment.

The size of the seminiferous tubules and the development of spermatogenesis with respect to body weight paralleled the changes in size of the secondary sex organs, supporting the conclusion that in the mice from the experimental populations there was either a reduction in the amount of gonadotrophin produced or interference with its action. Baker, Schairer, Ingle, and Li (1950) stated that C-11 oxygenated cortical steroids probably exert a suppressive action on the male reproductive organs. Therefore, some direct interference by adrenal steroids must be considered.

The thymus glands of experimental mice weighing less than 16 grams were heavier than their controls, indicating a suppression of androgen production (Burrows 1949). Thymic involution coincided with the onset of rapid growth of the reproductive organs and involution of the X-zone in the experimental mice. The thymus weights were well below the control weights in the heavier body weight intervals. Such marked thymic involution indicates an increased adrenocortical secretion (Selye 1950; Ingle 1950), especially as there is no evidence that androgen levels in the experimental males exceeded those of the controls. The seminal vesicles did not surpass their controls in size. The preputial glands were larger than their controls only in male mice weighing more than 28 grams. The increased preputial weight may have resulted from stimulation by ACTH in addition to normal androgen stimulation in these mice.

Organ measurements from the intermediate populations were approximately midway between those for the control and high populations. The amount of stress and reproductive suppression in these mice were correspondingly about half the amount in the high populations.

The data for the female mice lead to the same

conclusions as those for the male mice. The experimental adrenal weights were heavier than their controls in female mice weighing more than 16 grams, although there was some overlap between the control and experimental adrenal weights below this body weight. However, the zona fasciculata was wider in the experimental mice than in their controls for every body weight interval. Delayed involution of the X-zone produced the marked peak in adrenal weight of experimental females weighing 19-21.9 grams. First pregnancies were apparently delayed with respect to the controls in females from the experimental populations. There appears to have been a delayed onset of puberty in the female mice, as well as in the males, as a result of a suppression of gonadotrophic activity.

The preputial glands of the experimental females were heavier than their controls for all body weights, indicating an increased secretion of ACTH, decreased secretion of estrogens, or both. These glands from the intermediate populations were lighter than those from the high populations and heavier than their controls suggesting hormonal alterations midway between the two extremes.

A delay in the onset of puberty would account partly for the declining birth rate with increasing population size. In addition there was a decline in total litter size, which also may have been due to a partial suppression of the hormones of reproduction. The adrenocortical steroids may have reduced productivity further by direct suppressive action. Cortisone is known to increase intrauterine mortality in pregnant rats (Seifter, Christian, and Ehrich 1951). Increased infant mortality with increased population size is believed to have resulted from a failure in lactation for several reasons: stress is known to suppress lactation (Selye 1950), there is evidence of a decreased gonadotrophic activity, and the young were found unharmed but with empty stomachs. Proof of a failure of lactation will have to await further experimentation.

The growth curves of these mouse populations were fairly typical of the sigmoid curves described as characteristic for population growth (Allee, Emerson, Park, Park, and Schmidt 1949). These curves were mainly functions of the birth and infant survival rates, as adult mortality was negligible.

Increases in maximum population size occurred simultaneously with decreases in adrenal weight with successive experiments, and may have been related to each other. There may have been a gradual decline in aggressiveness in these mice during captivity, although verifying observations were not made. It is known that keeping wild mammals in captivity will result in a reduction of adrenal weight, primarily by a decrease in the amount of adrenocortical tissue (Rogers and Richter 1948; Christian and Ratcliffe 1952).

The results of the experiments with freely growing populations of wild mice indicate that in both sexes there was hypertrophy and hyperplasia of the adrenal cortex, especially of the zona fasciculata, and a suppression of reproductive function related to population size. The adrenal changes were more pronounced in the male than in the female mice. These results were indicative of an amount of stress in proportion to population size. In response to the stress there was an increased secretion of adrenocorticotrophin with a decreased production of gonadotrophin, interference with its action, or more likely both. These experiments by themselves are not proof that such a relationship between population size and stress exists, but the results are supported by data from a large number of experiments with populations of fixed size (Christian 1955a, b).

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Summary

Experimental populations of house mice (*Mus musculus*) were allowed to develop from a few pairs in large cages with food, water, cover, and nesting material in excess. Four populations were allowed to grow until population growth approached zero. Two populations were terminated at an estimated one-half maximum size. There was a steady decline in infant survival and birth-rate with increasing population size until both approached zero.

The adrenal weights of males from the high populations averaged 25% greater than their pair-isolated controls, while those from intermediate populations averaged 12% greater. The female adrenals from high populations were 7% greater than their controls for all body weights, and 14% greater if only females weighing more than 16 grams were considered. The adrenals of female mice from the intermediate populations averaged 7% greater than their controls. The increased adrenal weights were associated with hyperplasia and hypertrophy of the cortical zona fasciculata and delayed involution of the X-zone. The latter was attributed to a delayed onset of puberty which

in the males was also reflected in delays in thymic involution and development of the preputial glands, seminal vesicles, and testes. The experimental female preputial glands were heavier than their controls, which was attributed to stimulation by ACTH.

The productivity of the experimental female mice was reduced at least 31% from the control level, as determined by autopsy examination.

These results coincide with those from experiments with populations of fixed size, and were interpreted as follows; with increasing population density there are increasing levels of stress which are reflected by adrenocortical hypertrophy and reproductive suppression in both sexes of mice.

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NIGHTLY UNREST IN CAGED MIGRATORY SPARROWS UNDER OUTDOOR CONDITIONS[1]

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INTRODUCTION

The phenomenon of nocturnal activity, or *Zugunruhe,* in caged migratory birds has been known and studied in Europe for some time and has been regarded, as the German name indicates, as an expression of the migratory "urge." In America this nightly unrest has only recently begun to be investigated. Eyster (1952, 1954) found that it occurred in three species of migratory fringillids, *Junco hyemalis, Zonotrichia albicollis,* and *Zonotrichia leucophrys,* under conditions of temperature and photoperiod simulating those at which these birds normally migrate and that it did not occur in the nonmigratory *Passer domesticus* under the same conditions. Eyster described the effects of temperature on the daily activity rhythms of these birds, finding that the activity levels generally were depressed by either very high or very low temperatures and that between the extremes the level increased directly with the temperature. A decrease in the activity levels at the time of molt was also found. Eyster concluded that nightly unrest is an indicator of the migratory condition and that it can be equated with the actual nocturnal migratory behavior pattern exhibited by wild birds.

Farner and co-workers (1953a, 1954) have demonstrated the presence of nightly unrest in a migratory race of the white-crowned sparrow, *Zonotrichia leucophrys gambelii,* during the spring migration period under outdoor conditions and have correlated it with changes in body weight, fat deposition, molt and testicular development. In the nonmigratory Clark nutcracker, *Nucifraga columbiana,* nightly unrest was found not to occur at any time of the year (1953a).. Another important discovery by these workers is that high environmental temperatures induce nightly unrest in the white-crowned sparrow even at short photoperiods (1953b). This appears to weaken the supposition that nightly unrest is strictly associated with true migratory behavior and Farner *et al.* state (1954) that the investigation of *Zugunruhe* as a tool in the study of the physiology of migration must be applied very cautiously.

The investigations of *Zugunruhe* in Europe have been extensively reviewed by Palmgren (1944, 1949), Farner (1950), Eyster (1954) and others. These studies have also indicated some discrepancies between nightly unrest and actual migratory activity. In most of the species investigated the unrest begins in the spring at about the normal time of migration but continues throughout the breeding period, often until the onset of the post-nuptial molt. In the fall the unrest again appears at about the normal migration time but in many cases continues far into the winter. Many of the investigations were conducted under unnatural or unstated conditions of temperature and photoperiod and the results are thus difficult to interpret.

The present study was undertaken in connection with an experimental investigation of the role of the gonads in the physiology of migration in the white-throated sparrow. It was desired to use nightly unrest as one indicator of the migratory condition, but since there was considerable question of its reliability as such, it was decided to investigate it in newly captured migrating birds under outdoor conditions. This study was begun in the fall of 1951, and in the early spring of 1952 it was enlarged to a more intensive investigation of the relation of seasonal changes in activity to those in body weight, molt, and later, fat deposition and energy intake, under outdoor conditions. It was believed that the climatic conditions to which the birds were exposed at Champaign, Illinois, would not be greatly different from those to which wild birds are exposed and that any physiological changes caused by these conditions would be similar to those of wild birds. Thus the exact relationships of nightly unrest with the migratory periods, and with other presumed indicators of the migratory condition, could be determined. For comparison with the white-throated sparrow, two other species, the tree sparrow and the slate-colored junco, with different migratory habits, were also studied.

Observations were made on birds confined in individual activity cages in an outdoor aviary in the fall of 1951, and continuously from March, 1952 until the end of July, 1953. In 1951 only the activity was studied; beginning in 1952 regular observations were also made on body weight and molt. Fat deposition was studied for the ten-month period from October, 1952 through July, 1953, and food consumption (metabolized energy

[1] Contribution from the Department of Zoology, University of Illinois, Urbana, Illinois, and the Department of Biology, Fisk University, Nashville, Tennessee.

intake) for the six-month period from February through July, 1953.

The number of birds used was necessarily small, since only four to six activity cages could be run at any one time. Six male and six female white-throated sparrows, *Zonotrichia albicollis,* were used, the periods of observation varying from one week to sixteen months. Three male and one female tree sparrow, *Spizella arborea,* were also observed, and one male slate-colored junco, *Junco hyemalis.*

The white-throated sparrow is a migrant at Champaign, passing through in late April and early May, and from late September until November. Seibert (1949) plotted its breeding and wintering ranges and the approximate isotherms and photoperiods of the boundaries of each. Comparison of the appropriate Champaign photoperiods with the summer photoperiod of the southern boundary of the breeding range and winter photoperiod of the northern boundary of the wintering range, reveals only a few minutes' difference in both cases. The monthly mean temperatures at Champaign during the mild winter of 1952-53 were all above O°C, the isotherm which approximately delimits the northern boundary of the winter range. On the other hand, the 1952 and 1953 summer temperatures at Champaign were considerably above 21°C, the isotherm coinciding with the southern boundary of the breeding range. The white-throated sparrows, then, were exposed to near-normal photoperiods in this study and to near-normal temperatures except during the summer.

The same is true for the junco, since it is common at Champaign from late September to late April, and the southern boundary of its breeding range is about the same as that of the white-throated sparrow, although its range extends much farther north.

Tree sparrows are common at Champaign from November through April. However the breeding range lies much farther north than those of the other two species, and the conditions of photoperiod and temperature to which these birds were exposed in the summer were far from normal.

The constant aid and advice of Dr. S. C. Kendeigh is gratefully acknowledged, and thanks are due him and Dr. N. W. Riser for reading and criticizing the manuscript.

Methods

In order to observe simultaneously the phenomena of activity rhythms, body weight changes, fat deposition, molt, and food consumption, the intensive study of any one of which would be very time consuming, it was necessary to invent several indices and short-cut methods of analysis.

Activity was recorded continuously by a mechanical method similar to that described by Farner and Mewaldt (1953a), but independently devised. The birds were kept permanently in individual activity cages which registered changes in position of the birds. Until September 1952 the cages were such that only movements involving the perch were recorded. After September 15, 1952, an improved type of cage was used which had a movable bottom, and both the bottom and the perch were suspended from a microswitch on the top of the cage. The construction of this cage was such that the bird was nearly always forced to strike either the bottom or the perch when it changed position; hence a relatively high proportion of the total activity was recorded, and, more important, the cage was easily maintained in working order. The differences between the two types of cages in the proportion of activity recorded and also the unavoidable differences in sensitivity between the individual cages of each type were cancelled out to a large extent by the method of analysis described below.

The recording mechanism consisted of a series of ink-writing signal magnets and a slow speed kymograph. No timing marker was used; the time was simply indicated at the beginning and end of each 24-hour record. Frequent checks insured that the kymograph ran at a constant rate of speed, 7.7 cm per hour, at all times.

In analyzing the records a tape was used upon which had been constructed a scale consisting of hourly divisions, each subdivided into ten equal six-minute spaces or "units." The scale was laid along the record so that the times of the beginning and end of the record matched the equivalent times on the scale. The number of time intervals in which activity occurred in each hour was then transcribed. After adjusting for gaps in the records and for "weeks" of different lengths (*e.g.* six, seven, or eight days to conform to the times of weighing and examination of the birds) the data were expressed in terms of the average number of units of activity per night and per day, for each week of the year. Thus the activity values used in this paper are indices of the total activity during the light and dark periods. The upper limit of the index varies with photoperiod, *e.g.* in late June the maximum possible daylight activity would be 160 units (16 hours x 10 units per hour) and the maximum possible nightly activity would be 80 units.

Since the basic time unit of six minutes was fairly large and since one mark of activity in a

unit counted the same as a large number of marks, error due to the differential sensitivity of the cages was minimized.

Body-weight, fat-deposition, and molt-intensity determinations were made at approximately weekly intervals. The values obtained at the beginning and end of each week were averaged to give a value corresponding to the weekly activity value.

The body weights were measured to the nearest tenth of a gram and represent mid-afternoon weights in all cases. Fat deposition and utilization were observed by means of a system of fat classes, adapted from those used by McCabe (1943), Blanchard (1941), and Wolfson (1945). Five classes were used as follows:

Class 0	None	No fat visible in the furcular depression or on the abdomen.
Class 1	Little	Noticeable deposits in the furcular depression.
Class 2	Medium	Furcular depression just filled with fat; small deposits on abodmen.
Class 3	Heavy	Furcular region bulging with fat; abdominal muscle entirely hidden by subcutaneous fat.
Class 4	Very heavy	Furcular region bulging greatly; abdomen much distended by peritoneal fat.

This system of classes provides an index of the subcutaneous and peritoneal fat deposits. The criteria are fairly objective and statistical analysis of the relationship between the fat classes and body weight showed that the successive classes represent definite increments of fat, although the increments are not exactly the same between all classes. The sequence of deposition is indicated by the above description of the classes; the sequence of utilization was just the reverse of deposition, as has been noted also by Wolfson (1954). There was no observable difference in the sequence or relative extent of fat deposition and utilization in the three species studied nor in the sexes of the same species.

At the time of weighing, the cage pans were cleaned and brief statements were recorded regarding the number of molted feathers in the pan. When the birds were weighed they were also examined quickly but completely for the presence of fresh sheathed feathers, and the relative numbers and general distribution of these were noted, using such terms as "none," "few," "some," or "many." In analyzing these data an arbitrary scale was established which attempted to evaluate the extent of the molt in terms of the relative sizes of the feathers and body areas affected. In this scale the body was divided into: head (including throat and neck), trunk, and flight feathers. "Many" regenerating feathers on the head was assigned the value of 3, "some" 2, and "few," 1; for the trunk the respective values were 4, 3, and 2; and for the flight feathers 5, 4, and 3. No distinction was made among the kinds of feathers in the cage pans. "Many" was given the value of 3, etc. The molt intensity value for a particular date was obtained simply by adding the appropriate figures from this scale. Thus a value of 0 indicates no molt, while a value of 15, the highest possible, indicates extensive loss and regeneration in most of the feather tracts. It should be mentioned that in the case of primaries, one sheathed primary per wing was considered "few"; two, "some"; and three or more, "many."

The metabolized energy intake was measured by an abbreviation of the method employed by Kendeigh (1949) and Seibert (1949). Weighed amounts of food (University of Illinois Baby Chick Mash 521) of known constant composition and caloric value were provided each bird. At the end of three or four days the unused food and excrement were collected, dried at 100°C for two days and weighed together. The difference in the dry weights of the food provided and the total wastes was considered to represent the amount of food metabolized during the period. This was expressed in calories by multiplying by 4.3, the caloric value per gram of the dry food.

Kendeigh and Seibert manually separated the excrement from the waste food and made separate caloric determinations of each.

Since it is known that the caloric value of the excrement is somewhat lower than that of the food, the main assumptions made in this short-cut method were that the proportion of excrement in the wastes was relatively small and that this proportion remained constant. A test of the difference between the long and short methods, involving 16 comparisons, showed that the short method gave results averaging only 1.8 percent lower than the long method and that the difference was not statistically significant. Since some doubt remains as to the absolute accuracy of this method, only general trends in the energy intake are discussed in this paper.

The activity cages in which the birds were kept were located in a large screened outdoor aviary, fully protected from cats, mice and other possibly disturbing factors. Occasionally the birds were briefly disturbed by humans near the aviary in the day, but the effects of this on the activity records were slight and were rendered negligible by the methods of analysis. The birds were almost never disturbed at night, and when they were the period of disturbance was not included in the analysis of the activity record.

TABLE I. Capture data and observation periods of birds

Band Number	Sex	Date of Capture	Disposition and photoperiod after capture	Outdoor observation period*	Number of days
White-throated Sparrow					
113031	M	Oct. 23, '51	Indoors, 9 hours	Nov. 5-Dec. 13, '51	38
113036	M	Nov. 1, '51	Indoors, 9 hours	Nov. 12-Dec. 3, '51	21
113033	M	Oct. 26, '51	Indoors, 9 hours	Mar. 31, '52-July 28, '53	484
113200	M	April 30, '52	Indoors, Natural	May 12-Dec. 15, '52	133
113123	M	Oct. 17, '52	Outdoor aviary	Nov. 5, '52-July 28, '53	247
113115	M	Oct. 17, '52	Outdoor aviary	June 16-23, '53	7
113134	F	Oct. 13, '51	Indoors, 9 hours	Oct. 17-Dec. 13, '51	57
113035**	F	Oct. 29, '51	Indoors, 9 hours	Nov. 12-Dec. 3, '51	21
113030	F	Oct. 23, '51	Indoors, 9 hours	Mar. 31, '52-July 28, '53	484
113135	F	Oct. 16, '52	Outdoor aviary	Oct. 20-Dec. 15, '52	56
113124	F	Oct. 17, '52	Outdoor aviary	Oct. 27, '52-July 28, '53	247
113129	F	Oct. 22, '52	Outdoor aviary	June 9-23, '53	14
Tree Sparrow					
43555	M	Mar. 14, '52	Indoors, Natural	Mar. 19, '52-June 7, '53	445
43580	M	Mar. 14, '52	Indoors, Natural	Mar. 19-Aug. 3, '52	111
43558**	M	Feb. 27, '52	Indoors, Natural	Aug. 3-7, '52	4
43571**	F	Feb. 27, '52	Indoors, Natural	June 23-July 28, '53	35
Junco					
17420	M	Nov. 1, '52	Indoors, Natural	Dec. 15, '52-July 28, '53	206

*Activity—daily records from Nov. 5 to Dec. 13, 1951, and from March 19, 1952 to July 28, 1953.
Body weight—weekly determinations from March 19, 1952 to July 28, 1953.
Molt—weekly determinations from June 4, 1952 to July 28, 1953.
Fat class—weekly determinations from Oct. 12, 1952 to July 28, 1953.
Metabolized energy—semi-weekly determinations from Feb. 4, 1953 to July 28, 1953.
**Not included in averaging data. See text.

The aviary was partially protected from north and west winds by the walls of a building but rain blowing in from the east occasionally reached the cages. In the winter the cages were exposed to direct sunlight throughout the mornings, but in summer nearby vegetation shaded them except in the very early morning hours. Lights from nearby buildings had little, if any, effect on the light intensity at night.

All of the birds used in this study were trapped from wild populations in the vicinity of Champaign. Most of them were kept indoors for a few days before being placed in the outdoor cages. A few were placed directly in a second outdoor aviary, near the one in which the activity cages were located, and later transferred to the activity cages for observation. A few were used that had been indoors for long periods of time.

Table I summarizes the history of each of the birds used. The data obtained from three of the birds were not used in the analysis of the results. Number 113035 was in weak physical condition when placed under observation and did not improve. Tree sparrow 43558 died after only four days in the activity cage, and 43571 had been previously used in another experiment.

Temperature was recorded in the aviary by means of a thermograph. Other weather data were supplied by the Urbana weather station, located about 100 yards from the aviary. All photoperiods mentioned in this paper include civil twilight in both morning and evening.

RESULTS

Daily Rhythm

Since the chief objective of this study was to determine seasonal rhythms or changes, no detailed analysis was made of the daily activity patterns. However, on the basis of the seasonal rhythms observed (Figs. 2, 3), certain weeks of the year were selected to represent the important phases of the annual activity cycle, and the average hour-to-hour patterns of these were studied. A brief description of these patterns may be in order here. Figure 1 illustrates the patterns in the male white-throated sparrow.

There was very little species or sex difference in the patterns of activity, either in the daylight or at night. The birds became active abruptly at about the time of civil sunrise and the maximum level for the day occurred within the next two or three hours. During the late morning and in the afternoon the activity level decreased slowly but steadily due to the occurrence of short rest periods. Generally there was a brief burst of intense activity at the end of the day, which did not last long enough to show up in the hour-to-hour analysis, except in the junco, which had a tendency to show a late afternoon peak of activity in addition to the morning peak. In all birds the activity ceased

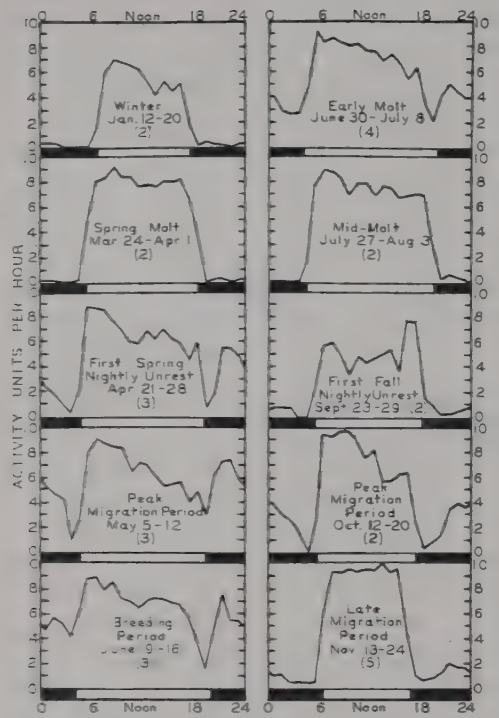

FIG. 1. Diurnal activity rhythms in caged male white-throated sparrows during selected periods representing some of the phases of the annual activity cycle. Solid bar = dark period; open bar = light period including civil twilight. Each curve based on recordings of two to five birds. · Curve dated Sept. 23-29 based on poor recordings.

abruptly close to the time of civil sunset. This pattern showed little seasonal variation, except in the levels attained.

If nightly unrest were not exhibited the activity levels during the dark period were near zero. Occasional scattered marks sometimes occurred on the records, indicating brief awakenings of the birds.

The nightly unrest, when present, nearly always followed a simple definite pattern. Following the cessation of the daylight activity, there was a period of rest lasting from about half an hour to two hours, being shorter in the spring than in the fall. After this rest period the birds, in the spring, abruptly became active and continued so for several hours, reaching a peak level from 21 to 23 hours. In the fall the rest period was longer and the increase in activity more gradual, with the peak of unrest occurring at about the same time as in the spring. After the peak activity the level declined as the birds alternated brief periods of rest with periods of activity. There was usually a longer rest period just before civil sunrise. Differences in the total activity during the dark period were a result of the lengthening or shortening of these periods of activity and rest.

Seasonal Changes

The seasonal trends and levels exhibited by birds of the same sex and species were quite uniform, the main individual variation being relatively slight differences in the timing of such events as the beginning of molt or nightly unrest as shown in Table II. Therefore, even though the number of birds was very small, it was decided that the results could be shown accurately, as well as most meaningfully, by averaging the data for birds of the same sex and species for each week of the year. These results are shown graphically in Figures 2 and 3. The writer is aware of the dangers involved in drawing conclusions from the means of so few values, or from single values, and will attempt to indicate those portions of the curves which are especially subject to error due to individual variation. It must be emphasized that each point on these curves represents a value for an entire week.

White-throated Sparrow. The white-throated sparrow underwent two periods of molt during the year, which corresponded in all observable respects to the normal prenuptial and postnuptial molts. The spring molt began in March on the head and throat, extended to the trunk, mainly the breast, in late March, and in early April became restricted again to the head and throat where some new feathers continued to appear until late April or early May. This molt was studied only in 1953, in two males and two females, and there was considerable individual variation both in the timing and intensity, which is not indicated in Figure 2 (see Table II).

The entire summer molt was observed in two males and one female in 1952 and the early part of it in two males and two females in 1953. This was a complete molt beginning in early July on the back and rump and quickly extending to the primaries and underparts. The rectrices and secondaries were molted in early August, while the trunk molt was still in progress, and the head feathers and outermost primaries in late August and early September. There was little individual variation in this molt, but there was some difference between the two years in respect to its beginning. In 1952 it began about ten days later than in 1953.

The body weight was fairly high in mid-January, 32 grams in the males and 30 in the females, but declined from then until early March to a low point of under 26 grams in both sexes, which

TABLE II. Dates of some significant events in caged outdoor birds

Band Number	Year	Spring Molt		Fat	Spring Nightly Unrest		Summer Molt		Autumn Nightly Unrest	
		First observed	Last observed on trunk	Class 4 attained in spring	First night	Last night	First observed	Last observed on trunk	First night	Last night
White-throated Sparrow										
113031	'51	—	—	—	—	—	—	—	—	Nov. 14
113036	'51	—	—	—	—	—	—	—	—	Dec. 2
113033	'52	—	—	—	Apr. 25	July 11	July 16	Aug. 26	Sept. 21	Nov. 23
113200	'52	—	—	—	—	July 25	July 18	Sept. 8	Oct. 1	Nov. 29
113123	'52	—	—	—	—	—	—	—	—	Dec. 12
113033	'53	Mar. 3	Apr. 1	Apr. 28	Apr. 22	July 7	July 8	—	—	—
113123	'53	Mar. 17	Apr. 1	Apr. 28	Apr. 22	July 20	July 8	—	—	—
113134	'51	—	—	—	—	—	—	—	—	Dec. 8
113030	'52	—	—	—	May 4	July 16	July 20	Aug. 26	Sept. 17	Dec. 5
113124	'52	—	—	—	—	—	—	—	—	Dec. 6
113135	'52	—	—	—	—	—	—	—	—	Dec. 6
113030	'53	Mar. 10	Apr. 1	Apr. 28	Apr. 24	July 8	July 8	—	—	—
113124	'53	Mar. 24	Apr. 7	Apr. 28	Apr. 30	July 20	July 15	—	—	—
Tree Sparrow										
43555	'52	—	—	—	Mar. 28	*	July 13	Aug. 26	*	Nov. 28
43580	'52	—	—	—	Apr. 3	*	July 18	—	—	—
43555	'53	Mar. 17	no trunk molt	Apr. 7	Mar. 21	—	—	—	—	—
Junco										
17420	'53	Mar. 10	no trunk molt	Apr. 7	Mar. 29	July 7	July 8	—	—	—

*Nightly unrest continuous throughout molt period.

coincided with the period of increasing intensity of the spring molt. After this molt had passed its peak in early April the weight increased again rapidly, the greatest gains occurring in the third and fourth weeks of April in 1953 and in the first week in May in 1952. This difference is believed to have been due to the abnormal history of the two birds (113033 and 113030) observed in 1952. These birds had been kept over winter on a short photoperiod and were not exposed to natural day-lengths until March 31. In any case, although the most rapid gains occurred at the same time in the males and females, the increase in the female weights began a week later than in the males in both years and was not as great. The peaks (33-34 grams in the males and over 31 grams in the females) occurred at the same time in early May. From mid-May until late July, the weights declined gradually, reaching a second minimum for the year at about 28 grams in late July, when the summer molt was increasing in intensity. In 1952, there was considerable variation between the three birds observed, as well as some fluctuation for each bird. In 1953 the low point was much more uniform and somewhat lower (26 grams as compared to 27-30). After the molt began to wane in late August, the weights of the males rose slightly, dropped a little in September and then increased steadily to reach a peak of over 33 grams in late October. The weight of the one female observed at this time rose slightly in late August and early September, then decreased to a low point of 27 grams in October. It increased in late October and by mid-November had reached the level (29-30 grams) of two newly captured females which were added to the outdoor group at that time. In late November and early December the weights of the males decreased rapidly to 30 grams, and those of the females slightly to 28-29 grams. In late December and early January the weights in both sexes increased to the mid-winter levels.

The fat-class curves follow very closely the weight curves. In mid-winter the birds were in classes 2 and 3. In February and March the fat deposits declined, reaching class 0 in three of the four birds observed at this time of the year. In one female, 113030, the fat declined only to class 1. These minima in the curves coincided with the body weight minimum and the spring molt. In late April, fat was deposited rapidly in all of the birds with very little variation. This fat diminished slowly in late May, June and July. No fat determinations were made in the months of August and September. From mid-October until mid-November the males were in fat classes 3 and 4. There followed a decline to class 2 in late De-

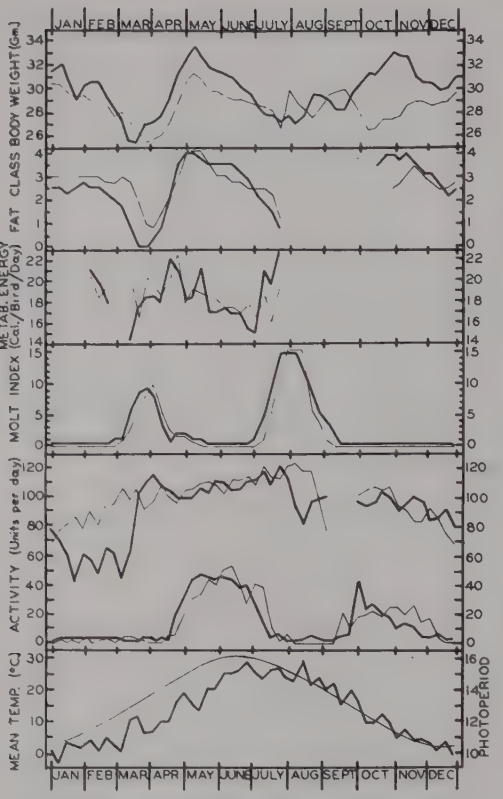

FIG. 2. Seasonal physiological changes in caged white-throated sparrows at Champaign, Illinois, in relation to weekly mean temperatures and photoperiod. Heavy lines = males; light lines = females. Upper activity curve = daylight activity; lower curve = nightly unrest. All points are averages based on two to five birds except in the curves for females from August 1 to October 15.

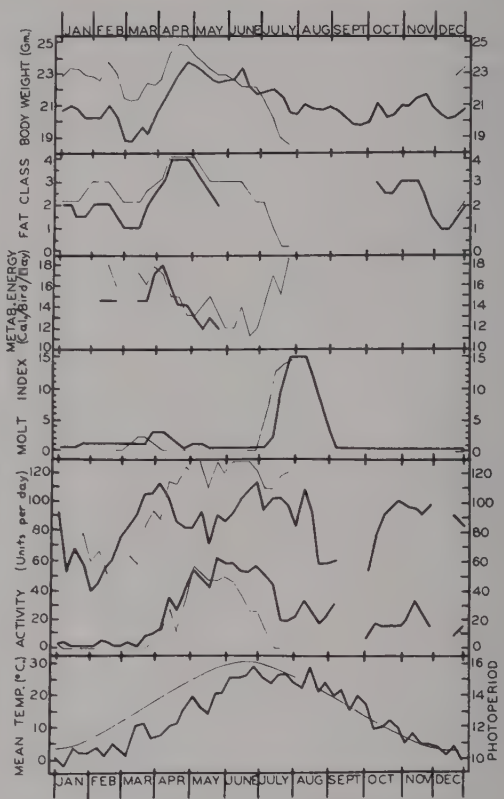

FIG. 3. Seasonal physiological changes in caged tree sparrows and junco at Champaign, Illinois, in relation to weekly mean temperatures and photoperiod. Heavy lines = male tree sparrows; light lines = male junco. Upper activity curve = daylight activity; lower curve = nightly unrest. Points in the body weight, molt and activity curves of the tree sparrow from March 20 to August 1 are averages based on two or three birds; all other points are single values.

cember and then a slight rise to the mid-winter levels. The trends for the female curve in November and December were the same as for that of the males.

The trend of metabolized energy intake in the male is fairly well defined. There was some decline during February which presumably extended into early March, when a succession of heavy rains with east winds dampened the cages and prevented the collection of these data for two weeks. This decline coincided with the weight and fat decreases. In March, coinciding with the spring molt, an increase occurred, which was closely followed by a further increase in April at the time of the rapid weight and fat gains. From early May until early July the energy intake declined slowly reaching a low point at the beginning of the summer molt. With the increasing intensity of the molt the metabolized energy intake increased very rapidly.

One of the two females studied exhibited considerable fluctuation in energy intake; the other showed a more uniform energy intake similar to that of the males. In Figure 2 the high value in the female curve in early March is questionable and it is believed that the only real difference between the male and female curves is that in July when the less extensive increase in the metabolized energy in the females can be correlated with the later molt in that sex.

Daylight activity varied directly with the length of the photoperiod as would be expected. However the greatest activity occurred in July and August and the least in January and February,

possibly indicating some influence by environmental temperatures. The males were less active than the females in late winter and in August, for which no explanation can be offered. In March the males abruptly changed from a low level of activity to a much higher level. This change coincided with the increasing spring molt and with a period of warm weather. That the molt exerted some influence is indicated by the fact that one of the birds molted later than the other and in this bird the shift in activity level was correspondingly later.

Nightly unrest was entirely absent in all of the birds from early December until late April. In 1952 the one male then under observation first showed nightly unrest on April 25, and the one female on May 4. In 1953 the two males became active on the night of April 22, one female on the night of April 24, and the other on the night of April 30. The nightly unrest pattern in all cases was well developed and fairly intense (20 to 30 units) on the first night of activity. In the first week or so after the first unrest occurred there were occasional nights of complete rest, but by the second week in May the birds were active every night, and the intensity had increased to about 50 units, a level which was maintained until early in July. In July the nights of unrest again occurred intermittently, the intensity of the unrest decreased to a certain extent, and shortly before or after the beginning of the summer molt it disappeared entirely.

The curve for the females in Figure 2 masks a considerable amount of individual variation in the intensity of this spring nightly unrest. The males were very uniform in this respect.

Activity recording in September 1952 was severely hampered by mechanical difficulties with the cages. Few records were obtained and most of these were unreliable in that only a small proportion of the total activity was registered. Thus, the first nights of unrest in the autumn cannot be definitely determined. The first observations of unrest were on September 17 in the female and on September 21 and October 1 in the two males then under observation. The activity on these nights was of the typical pattern, but was not as intense as on the first nights of activity in the spring. During October nightly unrest was present on most nights but never reached the intensity attained in the spring, and in November it became less frequent and less intense. The last nights of unrest in the late fall are shown in Table II. The males showed considerable variation, while the females were often active at night throughout November, and became inactive uniformly in early December.

Slate-colored junco. During the period in which it was observed the single junco exhibited seasonal changes very much like those of the male white-throated sparrows, except in timing. One striking difference was in the extent of the spring molt, which involved only some of the feathers of the chin and throat regions and was relatively brief. Possibly in correlation with this, there was no decided pre-molt decrease in the energy intake in February and March, and the weight and fat minima which coincided with the molt were not nearly as low, proportionately, as in the white-throat. The most rapid fat deposition and weight gain in the spring occurred in the first week of April, three weeks earlier than in the white-throated sparrows, and the peak weight occurred in the third week of April.

As in the male white-throats the daylight activity level was low in late winter but increased rapidly at the time of the spring molt. The first night of unrest was March 29; throughout April the unrest occurred intermittently, several consecutive nights of activity alternating with several nights of rest. In May and June it occurred every night.

With the beginning of the summer molt, which resembled that of the white-throated sparrows, the bird lost weight and fat rapidly, while the energy intake increased sharply. The nightly unrest declined in late June and was last observed the night of July 7.

Tree sparrow. The responses of the tree sparrows were quite different in many respects from those of the white-throated sparrows.

The spring molt, as observed in one bird in 1953, was restricted to the head and throat regions. It began in the middle of March and reached its peak intensity about April 1. The spring weight and fat minima were present but did not coincide with the molt, occurring in early March. There was a spring period of extensive weight gain and fat deposition, but this was more gradual than in the white-throats and began in mid-March before the spring molt. The energy intake, like that of the junco, showed no decline in February and early March, prior to the molt. The gradual weight decline in the summer was not visibly affected by the summer molt, which was in all respects like that of the white-throats. Instead, the body weight continued to decline steadily until late September. There was no pronounced autumn weight gain; a low peak occurred in November three weeks after the autumn peak in the white-throated sparrow. The mid-winter weight peak was still lower, not at all approaching the level of the spring peak, as it did in the white-throat.

The daylight activity level of the male tree sparrow, like those of the other species, was lowest in late winter. There was a steady upward trend in February, March and early April, followed by an abrupt decrease in late April and May, at the time of increasing nocturnal activity. As the nightly unrest decreased in June and July the daylight activity again increased. There was a sudden decrease in August, and a gradual increase in October, indicating a depression of the activity in the late summer following the molt.

Nightly unrest began in the spring of 1952 on March 28 in one bird and sometime before April 3 in the other. In 1953 it began on March 21 in the one bird observed. The unrest was at first intermittent, but in April it became more frequent and more intense, the peak levels in late May reaching nearly 65 units, as compared to 55 for the junco and 50 for the white-throated sparrow. The nightly activity decreased and became less frequent in July after the summer molt began, but did not cease entirely as in the other two species. This was observed in 43555 in 1952 and in 43571, a female, in 1953. In early November, there was a slight increase in the nocturnal unrest, and later in that month it became less frequent and disappeared. In late December there was some nightly activity in the one bird under observation, but it was not of the typical pattern. The bird rested for most of the night but became active two or three hours before dawn and continued so, without interruption, until late in the morning.

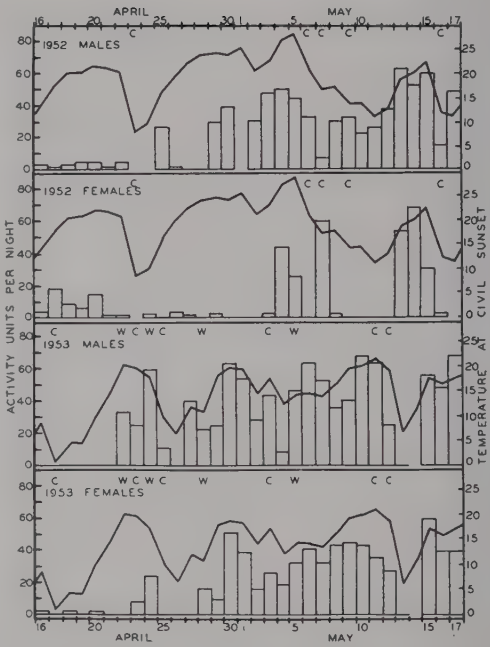

FIG. 4. Nightly unrest in white-throated sparrows in relation to weather in the springs of 1952 and 1953. Histogram = average nightly activity; curve = temperature in aviary; W = warm front; C = cold front. Gaps in base line of histogram indicate that no recordings were available.

Relation of Nightly Unrest to Weather Conditions

The intermittent occurrence of nightly unrest when it first began in the spring and fall and when it was diminishing in the late fall suggested that weather factors, as well as physiological changes, influenced it. Eyster (1954) found no clear correlation between temperature and nightly unrest in fringillids. Several European workers (Siivonen and Palmgren 1936; Wagner 1937; Palmgren 1937; Schildmacher 1938) have claimed such a correlation but their evidence is not conclusive. Another weather factor that might be involved is the movement through the area of the large masses of polar or tropical air or the "fronts" produced by them. There has recently been some evidence collected to show that many species of birds migrate rapidly or slowly in relation to these air movements. Bagg *et al.* (1950, p. 13) present the following hypothesis: ". . . during the period of spring migration, pronounced movement will take place into or through a given region during the interval between the passage of a warm front through that region and the subsequent arrival of a cold front." Accordingly, the nightly unrest data obtained in this study were analyzed for each night during portions of the migratory periods, and the average nightly indices for each sex and species plotted in relation to temperature and to the passage of cold and warm fronts through the Champaign area (Figs. 4-6). The temperatures shown are, in most cases the temperatures at civil sunset, extracted from the thermograph recordings made in the aviary. In some cases the Urbana weather station daily mean had to be used instead. The dates of the "fronts" were obtained from the U. S. Weather Bureau daily weather maps.

Figures 4 and 5 show that in the springs of both 1952 and 1953 the first night of activity of tree sparrows and white-throated sparrows occurred when temperatures were high or rising and during or shortly following the passage of a warm front. The first night of activity of the junco occurred at a moderate temperature. After the initial night of activity the intensity of unrest in all three species showed a fairly good correlation with these weather factors. Warm fronts and high temperatures were accompanied by intense unrest; cold fronts and low temperatures were accom-

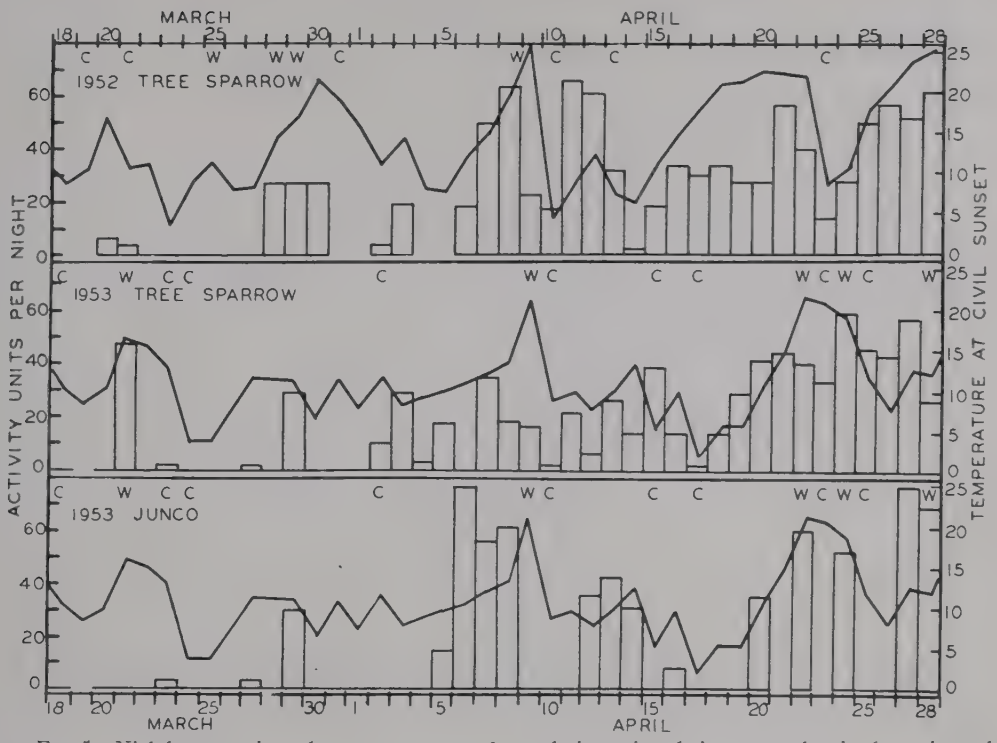

FIG. 5. Nightly unrest in male tree sparrows and a male junco in relation to weather in the springs of 1952 and 1953. Symbols as in Figure 4.

panied by little or no activty. The extremely high temperatures of April 9, 1952 and April 9, 1953, however, were accompanied by decreases in the nightly unrest of the tree sparrow and junco, although similar temperatures in late April and May had no such effect. In all three species there was a gradual increase in the amount of activity per night as the season advanced, so that by the end of the periods shown in Figures 4 and 5 a given temperature was accompanied by greater activity than it was at the beginning of these periods.

The significance of this relationship between temperature and unrest was tested by means of contingency tables which showed the frequency with which increases or decreases in temperature from one night to the next were accompanied by corresponding changes in the amount of activity. Three categories were used for each factor, namely, "increase," "no change" and "decrease." A temperature difference of less than five degrees F was considered "no change" as was an activity difference of less than five index units.

The results of this test are shown in Table III. The data for all three species were combined; the periods of time covered for each species are those shown in Figures 4 and 5. The relationship be-

TABLE III. Relation of intensity of nightly unrest to temperature changes

		Spring Nightly unrest			Early Fall Nightly unrest			Late Fall Nightly unrest		
		Increase	No change	Decrease	Increase	No change	Decrease	Increase	No change	Decrease
Temperature	Increase	41	52	15	8	14	1	9	35	11
	No change	44	63	38	19	16	9	22	49	22
	Decrease	5	28	29	3	11	7	7	29	7
		Chi-square = 29.024 $P < .01$			Chi-square = 13.306 $P \doteq .01$			Chi-square = 3.650 $P \doteq .45$		

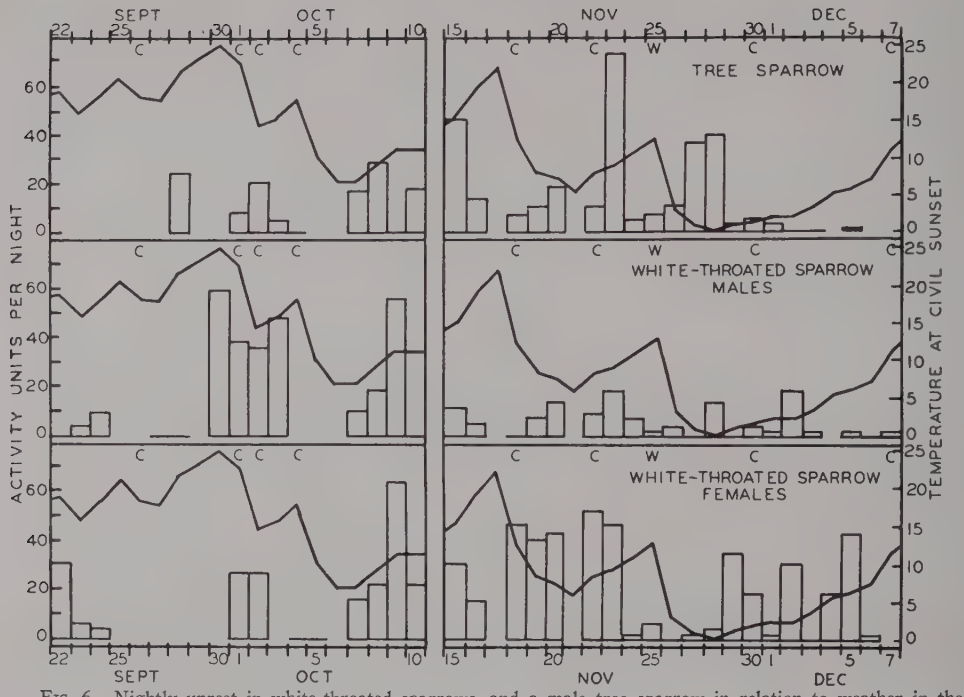

FIG. 6. Nightly unrest in white-throated sparrows and a male tree sparrow in relation to weather in the fall of 1952. Symbols as in Figure 4.

tween temperature and unrest is highly significant.

In the fall the situation is not so clear. Figure 6 indicates that in the early fall the intensity of unrest varies directly with temperature, as in the spring, while in the late fall no such relationship is evident. These data were analyzed by the method described above, arbitrarily dividing the season into two periods, September 16 to October 31, and November 1 to December 15. As shown in Table III temperature and unrest were significantly correlated in the early fall but not in the late fall.

DISCUSSION

The assumption that the seasonal changes observed in these caged birds would be similar to those of wild birds is partly confirmed by comparison with field studies. Odum (1949) and Odum and Perkinson (1951) have clearly shown the weight and fat changes in the white-throated sparrow on its wintering grounds in Georgia. The changes in the caged birds in Illinois corresponded very closely in timing and trend with those of the wild birds in Georgia, although the mid-winter weight levels were somewhat higher. The weight and fat minima associated with the spring molt, and the succeeding period of rapid weight-fat increase in the caged birds were consistent in all respects with the same phenomena in the Georgia birds.

There are no field studies with which to compare the summer conditions of weight and fat in this species. In one study of the white-crowned sparrow (Oakeson 1954) the birds had lost their fat deposits and were low in weight when they arrived on their breeding grounds. In the tree sparrow (see below) the birds are still fat but a rapid reduction occurs when breeding activities begin. In either case the gradual weight and fat loss during May and June in the birds in the present study was probably abnormal, and due to the absence of actual migration and breeding activity. The weight and fat conditions in wild birds during the summer molt and prior to the fall migration are unknown.

Baumgartner (1938) studied the weight cycle in the tree sparrow, from October to April at Ithaca, New York, and from late June through August at Churchill, Manitoba. The tree sparrows in the present study exhibited trends during the winter and spring similar to those found by Baumgartner, although the spring weight peak was much higher. However, Baumgartner's

March and April weights may have been influenced by the collection of transient birds from farther south, whose fat deposits had been depleted temporarily by long migratory flights (Wolfson 1945).

On its breeding grounds, Baumgartner found the tree sparrow to be fat and heavy before starting to breed, but very low in weight during the period of feeding young. The weight increased during the summer molt and was also moderately high during the fall migration. In the present study, the weight loss during the breeding season did not occur. The fact that the summer molt in the caged tree sparrows was not accompanied by a rapid weight reduction, as in the white-throated sparrows and junco, is consistent with the slight weight increase during the molt, found by Baumgartner. Apparently the energy demands of the molt are not as great in the tree sparrow as in the other two species, or else more "productive energy," as defined by Kendeigh (1949), is available.

The summer molt began at about the normal time in the white-throat and junco, but was apparently several weeks early in the tree sparrow, since Baumgartner did not find molting birds until August.

In their study of caged Gambel's white-crowned sparrows in late winter and spring, Farner *et al.* (1954) found changes in weight, fat, molt, and activity very similar to those found in the white-throated sparrow in the present study and very similar to those in wild Gambel's sparrows, as described by Blanchard and Erickson (1949).

From these comparisons it is concluded that, outside of the breeding period, the birds in this study were physiologically similar to wild birds and that the activity trends observed were also similar to those of wild birds.

Nightly unrest appeared in all three species in the spring at very nearly the times when the major migratory movements of these species begin. In fact, the first nights of unrest in the male white-throats in both 1952 and 1953 occurred within a few days of the first notable influx of wild migrants in the Champaign area. (This suggests the possibility that migrants passing overhead may have influenced the behavior of the caged birds. This cannot be ruled out; however it may be noted that these birds exhibited nightly unrest in the early summer when there were no wild migrants in the vicinity, and nightly unrest has been induced in indoor experiments where there is no possibility of such an influence.) Furthermore the unrest appeared at a time of rapid fat deposition, weight gain, and waning molt, in short, at a time when the birds were in a physiological condition typical of that at which wild birds begin to migrate, as observed by Odum, Baumgartner and others. Still further, weather changes affected nightly unrest in the spring in much the same way that they are reputed to affect actual migratory flights (Bagg *et al.* 1950; Williams 1950; Gunn and Crocker 1951; Imhof 1953; Devlin 1954), *i.e.* unrest was stimulated by warm fronts and high temperatures and inhibited by cold fronts and low temperatures. Likewise, in the fall nightly unrest began in the white-throated sparrow at about the normal time for the beginning of migration, and in the tree sparrow it reached a peak at about the time of the appearance of wild birds in the Champaign area.

The fact that nightly unrest occurred throughout the early summer beyond the normal migration period, can be explained by the abnormal physiology of the birds at that time. Judging from the weight and fat curves, the peak migratory condition occurred in early May in the white-throated sparrow, and in April in the tree sparrow and junco, at the normal times of migration. During the breeding period this condition gradually diminished but was not completely dissipated until the productive energy of the birds was diverted by the summer molt. Presumably in nature this productive energy is utilized in the early summer for the reproductive activities. Wolfson (1942) presents some evidence to show that caged birds (a migratory race of *Junco oreganus*) held in their winter range until the breeding period in June, will actually migrate when released. Apparently, then, the nightly unrest continued in the early summer because the birds remained in the migratory condition during that time.

The cessation of nightly unrest in the late fall occurred at about the normal termination of the migratory period. Fischer and Gill (1946) state that in the white-throated sparrow, "the height of the migration has passed by mid-November," implying that some movement takes place in late November.

It seems then that in this study nightly unrest was definitely associated with the migratory periods and with migratory physiological conditions. Under these environmental conditions it was a much more sensitive indicator than body weight or fat, since it varied from day to day according to weather conditions which presumably influence migration, and since it was more strictly confined to the migratory periods (weight and fat levels were high during the winter).

Two questions then remain. What is nightly unrest? Can it be generally used as an indicator of the migratory condition in experimental work?

The effect of environmental temperatures on both nightly unrest and daylight activity provides a clue to the answer to the first question. The results of the present study are in accord with those of Eyster (1954) who found that total daily activity in the white-throated sparrow varied directly with temperature. Eyster was unable to induce nightly unrest in birds held at low temperatures, even under the most favorable conditions of photoperiod. Further possible evidence is provided by the discovery by Farner and coworkers (1953b) that Gambel's white-crowned sparrows gain weight and fat and exhibit nightly unrest when exposed to high temperatures at a constant short photoperiod. (However, in the present study, white-throated sparrows under these conditions gained weight and fat but did not show nightly unrest.)

Nightly unrest seems to be affected adversely by energy-demanding physiological processes. It did not begin in the spring until the molt was nearly finished and the fat deposition was tapering off. With the onset of the summer molt nightly unrest disappeared completely in the white-throat and junco and was greatly reduced in the tree sparrow. Again in the fall it did not begin until the molt was completed and fat deposition was waning.

These considerations suggest that nightly unrest in caged birds is one of several outlets for productive energy (Kendeigh 1949). It is called into play when other outlets such as fat deposition and molting fail to make use of all the excess energy, and its intensity is directly related to the amount of such energy. That such a remarkable outlet is available to these species is due to the fact that they have evolved nocturnal flight as a part of their migratory behavior pattern. Just how closely the nightly unrest behavior pattern can be equated with the nocturnal flight pattern is open to question.

Since nightly unrest seems to be derived from the nocturnal flight behavior pattern, since it is always associated with physiological conditions similar to those in which birds are known to migrate, and since under near-normal conditions of temperature and photoperiod it is confined almost entirely to the migratory periods, it is concluded that it is a reliable indicator of the migratory condition.

Summary

1. Observations of seasonal physiological changes were made on captive migratory birds in an outdoor aviary at Champaign, Illinois from November, 1951 until July, 1953. Twelve white-throated sparrows, four tree sparrows and one slate-colored junco were observed for varying periods of time. The factors studied were: nocturnal and diurnal activity levels, as recorded mechanically; fat deposition; body weight changes; molt; and metabolized energy intake.

2. The seasonal changes in these factors are described and shown graphically.

3. Nocturnal activity began in the spring in all species at a time of rapid fat deposition and weight gain, and this occurred at the normal time of migration for each species.

4. Nocturnal activity continued during the normal breeding period and terminated (in the white-throated sparrow and junco) at the time of the summer molt, or was reduced (in the tree sparrow) during and after the molt.

5. Nightly activity in the fall began and ended in agreement with the normal time of migration.

6. In the spring and early fall nightly activity was enhanced by warm fronts and high environmental temperatures and inhibited by cold fronts and low temperatures. In the late fall there was no pronounced relationship with these weather conditions.

7. Nocturnal unrest is an outlet for productive energy in caged birds and appears when such energy is not entirely used for such other activities as resistance to winter cold, molt, fat deposition or breeding. The factors that determine which of these outlets is used at a given time remain to be determined.

8. It is concluded that nightly unrest may be used as a reliable indicator of the migratory condition in experimental studies.

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BEHAVIOR OF HOUSE MICE WITH REFERENCE TO FIXED POINTS OF ORIENTATION[1]

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INTRODUCTION

The literature on the ecology and natural history of animals in their native habitat suggests that the physical structure of the environment, including the kind and location of goal-objects, alters the use made of the environment. Previous investigations (Calhoun 1949) indicate that the physical structure of the environment may also modify social organization.

In natural habitats these physical structures are usually irregularly placed. This makes difficult the derivation of principles governing the control of orientation and social behavior by physical structures. Therefore it was decided to develop a stereotyped environment, in which groups of animals might live and remain under close observation. The stereotyping was to be limited to a situation in which distance was the major variable. This required that there should be a single place to which all individuals were regularly attracted, and from which a number of identical objects were located at regularly increasing distances. Two problems were to be studied: (1) the role of distance in determining the frequency of behavior or the presence of individuals, and (2) the role of distance in determining social behavior of individuals and the social structure of the group (Calhoun 1956). This report is confined to the first problem.

The frequency of observing individuals in different locations may be subsumed under the ecological concept of "home range." This concept has been developed with particular reference to rodents in their native habitats. Those species which have been studied are those which are easily trapped, and which, after being marked and released, readily re-enter traps. The concept of home range has primarily been confined to descriptions of the pattern formed by a succession

[1] The observations upon which this paper is based were obtained in the Division of Behavior Studies, Roscoe B. Jackson Memorial Laboratory, Bar Harbor, Maine. The study was supported in part by a fellowship from the National Institute of Mental Health.

of captures about the mean coordinate point of capture. This point has been termed the apparent center of activity by Hayne (1949), who presented the first systematic analysis of the pattern of captures. Further refinement of the concept of home range in terms of the probability of observing an animal about the center of its home range has been presented by Dice and Clark (1953) and by Calhoun, Casby, and Brant (manuscript). These analyses have shown that there is a decreasing probability of observing an animal at increasing distances from the center of its home range. A basic conclusion from these analyses is that the statistics of the system are stationary. That is to say, the animal does not move through space at random, but rather it orients about some theoretical point. To what extent this theoretical center of orientation represents some major goal or is merely an abstraction from the interaction of the attraction toward several neighboring goals is unknown.

Dice (1952) has reviewed the present status of our knowledge concerning home range from an ecological viewpoint. Despite the fact that he based his review in large part upon qualitative observations, it is apparent that certain conclusions regarding home range are valid. Foremost among these are the following: (1) Irregularities in the distribution of the physical components (goals) of the environment produce corresponding irregularities in the frequency of visitations. (2) As objects in the environment become sparser, the extent of the home range increases. (3) As the population density increases, the size of the home range becomes smaller.

From the above summary a restatement may be made of what is meant by home range: An animal moves about some central locus of orientation at which point the probability of its being observed per unit of area is greatest. Away from this central point there is a decreasing probability of observing the animal, although the presence of discrete goal-objects may produce local increases in the probability of visitation.

It will be noted that the concept of home range has been confined to the fact of the presence of the animal. Actually many different responses are expressed by an animal as it moves through its home range. Therefore, a refinement of the problem must include an analysis of the frequency distribution of specific types of behavior through space. The data in the present paper may best be viewed against the concept of home range.

It is here proposed that the mathematical term, "density function" be used to designate the frequency with which an animal or any specific behavior by it is observed through space. Density function specifically refers to the probability of an event per unit of area. This term will be so used in this paper.

Materials and Methods

Experimental Animals

House mice (*Mus musculus*) were selected as subjects for these experiments. Inbred strains of house mice were utilized from the stocks available at the Jackson Laboratory: DBA/2, C57BL/10, Small and Large.

The DBA mice are physiologically unstable as judged by the fact that there is a high incidence of breast tumors, and that they exhibit a marked susceptibility to audiogenic seizures. On the other hand, the C57 mice are characterized by a low incidence of breast tumors, and by a low susceptibility to audiogenic seizures. It was because of these marked differences between these two strains that they were selected for study. However, they were similar in size.

Size differences were marked between the strains Small and Large. The former weighs about 20 grams when adult, while the latter, which tends toward obesity, weighs about 40 grams.

As a contrast to these inbred strains, a few studies were conducted utilizing wild type mice trapped as adults on Parsons Island in Chesapeake Bay. This island lies southeast across the bay from Annapolis, Maryland.

Experimental Environment

At the time these studies were initiated, there were no adequate data on the home range of house mice. However, for other small rodents such as *Microtus* (Hayne 1949) and *Peromyscus* (Blair 1942) it has been shown that mice will roam over an area of at least 400 to 4,000 square meters. If house mice were to exhibit similar tendencies to roam, the laboratory area would certainly be confining, as the room available for the study measured only 5.3 by 7.3 meters, or 39 square meters of floor space, and was to be divided by screen walls so that two or four groups of mice could be studied simultaneously.

Normal patterns of space-utilization behavior could not be expected in such confined quarters; it was therefore necessary to structure the spaces in a fashion that would effectively increase their areas. Vertically structuring the environment was one such method. According to Schneider (1940), Benedict and Parmenter found for humans that the average amount of energy for walking up one flight of steps (15 steps, each 20 cm high) was 15 times that required for walking on the level the same distance as the vertical height of the stair-

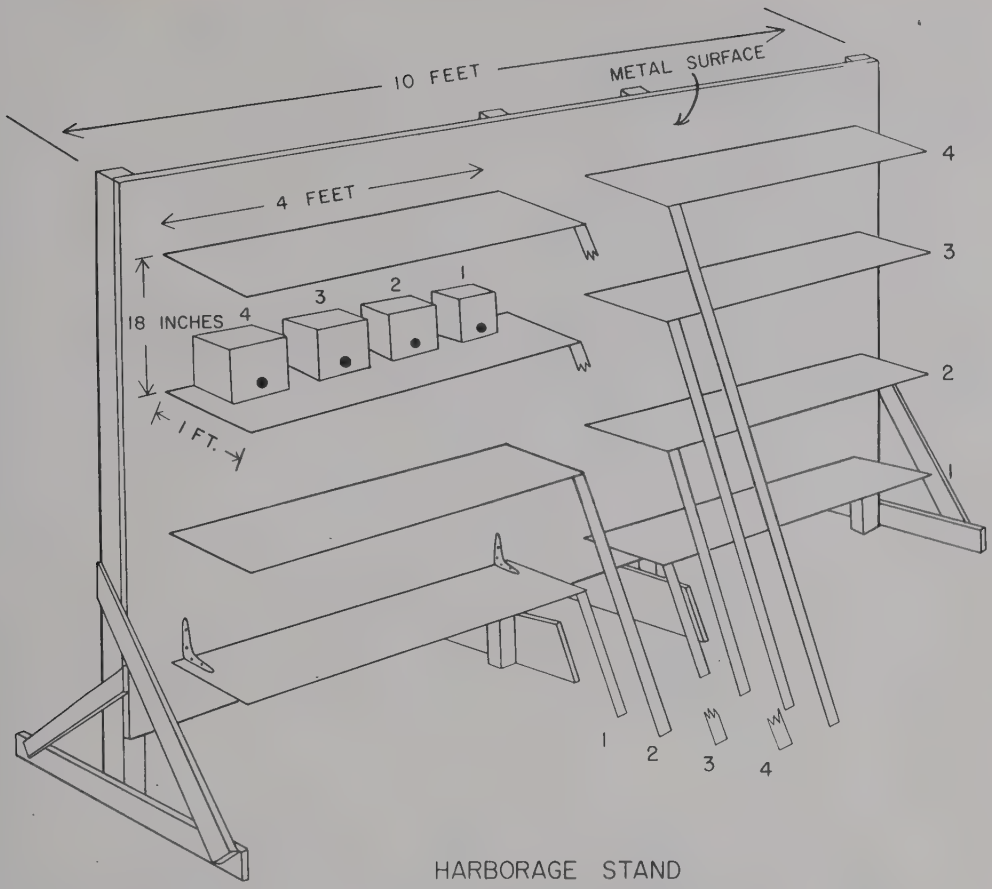

FIG. 1. Harborage stand. The shelves at the four levels were numbered from 1 to 4; the lowest shelf was No. 1 and the highest No. 4. A 37-mm-wide, screen-covered, wooden ramp connected the inner end of each shelf with the floor. Four wooden nest boxes, 150 mm on a side with a 25-mm opening on one side, were equally spaced along each shelf. The 16 boxes on the four left hand shelves were removed leaving these shelves bare during the history of DBA/2 Colony 2 and C57BL/10 Colony 2. Each nest box on the end of a shelf nearest its ramp was designated as No. 1 The other three nest boxes were numbered 2, 3, and 4, with No. 4 being at the end of the shelf farthest from its juncture with a ramp. Each box could be designated according to the level of the shelf, and its location along the shelf from the ramp. Thus 1-1 was the box nearest the floor and 4-4 was farthest from the floor. Each of the 16 positions were duplicated.

case. He also states that Fliesch found that the increased oxygen consumption of mounting one meter was equivalent to walking 17.7 meters on the level, and that descent of a staircase involves 33 per cent of the energy used for ascent. Thus, if the energy an animal expends in moving about its environment actually does influence the area which it covers, it might be anticipated that any condition which causes an animal to expend more energy in traveling a unit of distance will effectively reduce the area of its home range.

On the assumption that this hypothesis was correct, the environment into which the mice were to be released was partially vertically structured (Fig. 1). This vertical structuring consisted of a stand upon which shelves were placed at four levels. Each shelf was connected with the floor by a 37-mm width ramp at an angle of 60°. Since it is logical to assume that mice also expend more energy in traversing inclined routes of travel, this vertical structuring of the environment must have effectively expanded the available space. Two shelves were placed at each level to increase the numbers of different places that might be visited and also to reduce the amount of competition that might arise over simultaneous occupancy of a single level by the members of a colony.

Four nest boxes, each 15 cm square and with a

2.5-cm diameter opening, were placed along each shelf. This arrangement presented several opportunities on each shelf for entering boxes so that competition on any shelf might be reduced. This arrangement also amounted to a series of objects, each of which was at a successively greater distance from the end of the shelf to which the ramp was attached.

A pen, where food, water, and nesting material might be obtained was constructed on the floor opposite the bases of the ramps (Fig. 2). Access to this pen was by a single passage. Within this inclosure water was present in one or two one-gallon water fountains. There was a single hopper from which food could be eaten but not transported. Nesting material in the form of wood shavings, strips of paper towel, or cotton tow was made available in a single open-topped box.

The laboratory room was divided into four separate pens as shown in Figure 2. A meter high fence of window screen topped with a 45-cm

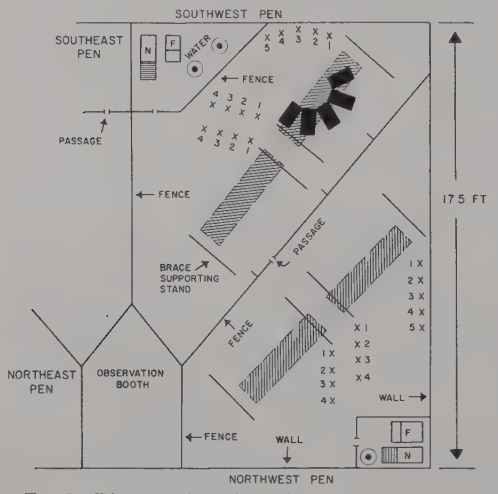

FIG. 2. Diagram of the floor plan of the pens in which the harborage stands were placed. The east pens were mirror images of the west pens. N = hopper of nesting material. F = hopper of food. X's represent the points at which ramps to the shelves on the harborage stand were attached to the floor. They were numbered in accordance with the level above the floor to which they led. Those X's numbered 1 to 5 are for the position of ramp bases in a set of experiments in which the stands consisted of five 2.75-m-long shelves. Note their proximity to the wall. The cross hatched area represents that portion of the floor shaded by the shelves above. The black rectangles are at the positions where the 150 x 150 x 300 mm nesting boxes, which also contained food and water, were placed when the mice were allowed to explore the 5 x 9 stand. Note that the floors of the pens are relatively unstructured. The food pen was removed from the northwest pen for C57 Colony 1B and from the northeast pen for DBA Colony 1B.

wide strip of sheet metal, which was at right angles to the fence, formed the barrier between pens. With the exception of the four braces supporting each stand and the bases of the ramps, the floor outside the food pen was completely unstructured. Other aspects of the environment included: (a) cork floors, (b) acoustic tile ceiling, (c) plaster wall with no windows, (d) thermostatically controlled constant temperature, (e) 12 hours of darkness from 6:00 A.M. to 6:00 P.M. with 12 hours of light from 6:00 P.M. to 6:00 A.M. This reverse light and darkness cycle enable observations to be made on these nocturnal animals during the normal outside daylight period. Temporarily turning on the lights when observations were made did not appear to inhibit the mice's activities.

As a result of initial studies utilizing the harborage stands with four shelf levels and four nest boxes on each shelf, it was decided to conduct a smaller series of studies on a more extensive harborage stand. A fifth shelf level was added. The two shelves at each level were joined. This made a single 2.75-meter shelf at each level. Nine nesting boxes were equally spaced along each of the five shelves. These two types of harborage stands will be referred to respectively as 4 x 4 stands, and 5 x 9 stands.

Procedures

The procedure for establishing a colony was as follows: One or two pregnant females were confined to a food pen. At the time the young were being weaned, the door to the food pen was opened, and they were permitted to explore the harborage stand. After a few days the mice began building nests in some of the boxes with nesting material they had transported from the food pen. At this time the mothers usually were removed.

DBA/2, Colony 1A, southeast pen. This colony primarily consisted of a litter of three males and three females born on October 10, 1949, in the food pen. At 22 days of age they were allowed access to the harborage pen from their previous confinement in the food pen. At 40 days of age their mother was removed. Between November 19 and April 13, 1950 ten litters were born but only three members of the seventh litter, born on March 22, 1950, survived.

DBA/2, Colony 1B. Four pairs of mice with litters born on the previous day were introduced into the northeast pen on March 21, 1950. On April 13, 1950 the door connecting the southeast and northeast pens was opened. This permitted the mingling of the nine Colony 1A mice in southeast pen and the twenty-one mice in the northeast pen. This combined group was designated Colony

1B. Observations of this group were continued to July 15, 1950.

DBA/2, Colony 2, northeast pen. This colony consisted of nine males and four females, who were released on November 15, 1950, at the age of 33 days, from their confinement to the food pen. Observations were continued to February 1, 1951.

C57BL/10 Colony 1A, southwest pen. On January 5, 1950, three males and three females of a litter born in the food pen 35 days earlier were given access to the larger pen. Their mother was removed a week later. Fourteen young of two litters were born on March 17 and 20, and all survived to April 13, 1950, the arbitrary date of termination of this colony.

C57BL/10, Colony 1B. Four pairs of mice with litters born on the previous day were introduced into the northwest pen on March 21, 1950. On April 13, 1950 the 20 Colony 1A mice of the southwest pen and the 33 mice of the northwest pen were allowed to intermingle by opening the door connecting the two pens. This combined group was designated Colony 1B. Observations were continued to July 17, 1950.

C57BL/10, Colony 2. The history of this colony closely parallels that of DBA/2, Colony 2, except that it was established in the southeast pen. The two litters were released from the food pen when 34 days of age on November 15, 1950. There were eleven males and four females. Observations were continued to February 1, 1951.

Strain Large Mice, Colony 1. Observations were made from August 8, 1950 to October 30, 1950. The colony consisted of two females and their twelve young.

Strain Small Mice, Colony 1. Observations were also made from August 8, 1950 to October 3, 1950. The colony consisted of two females and their eight young.

The harborage stands on which DBA/2 Colony 2 and C57BL/10 Colony 2 developed were modified from that of the other colonies. All the boxes were removed from the four left hand shelves.

The second modification to the harborage stand was made by adding a fifth shelf level, making each level a continuous 2.75-meter shelf, and by placing nine harborage boxes on each shelf. Adult males were allowed to explore this stand. Prior to release in the pens, each mouse had been isolated for several days or weeks in a separate wooden cage 15 x 15 x 30 cm. A 25-mm diameter door had previously been constructed in one end of each cage. These cages, with the doors opened, were placed on the floor facing the bases of the ramps (Fig. 2). One mouse at a time was left in a pen for approximately seven days. Nearly equal numbers of DBA, C57 and wild-caught Parsons Island males were represented. Isolated males were exposed to this stand for a total of 176 days. There was no detectable difference in the reaction between strains. Only the data for these isolated males are presented in this report (Figs. 5, 6) although several groups of males were released, and quite similar results were obtained.

Four items or events were counted with reference to the position upon the harborage stand where the mice were observed: feces, nesting material, places where the mice rested, and places the mice visited during periods of activity. Feces were counted separately for their location in nest boxes and for their location on the shelf beside boxes. The location beside boxes was designated as that space immediately in front of each box, as well as that space between it and the next more distally placed box, or in the case of the terminal box, as that space between it and the end of the shelf. Counts of feces, nesting material, and places of resting were made once each week for the DBA/2 and C57BL/10 1A colonies and for all the isolated males on the 5 x 9 stand. Similar counts for all other groups were made at intervals of approximately one month. Feces and nesting material were removed and discarded after each count. Qualitative accounts of the distribution of feces over the floor were frequently made on these occasions prior to sweeping them up. Systematic records were not made of all observations of places visited by mice during their periods of activity. However, a number of detailed accounts were assembled of the sequence of places visited by individual mice.

Results

Qualitative Observations

During every period of activity each mouse usually visited the food enclosure several times. Following eating or drinking each mouse normally spent some time at the base of the hopper or at the edge of the fountain. Such places were characterized by large deposits of feces. Feces were also concentrated in the food pen in the corners or near the vertical braces supporting the fence. These were places to which mice moved aside and stopped upon the entry of other mice. Upon leaving the food pen a mouse would do one of three things: (a) It proceeded around the room close to the fence or wall. Stops might occur at any point, although more frequently in the corners of the pen or at the vertical braces to the fence. At these places there were larger deposits of feces. From the periphery of the pen the mouse would proceed either directly to a ramp or to the area immedi-

ately below the shelves, from which it would then go to a ramp. Under the shelves, stopping and defecation occurred most frequently near the four braces of the stand. (b) A mouse would proceed directly from the food pen to one of the ramps. This was the most frequent approach to a ramp. (c) It would proceed directly to the portion of the floor under the central end of one of the sets of shelves where it would pause prior to returning and going up one of the ramps. During practically none of these movements did the mice stop at unstructured places on the floor, nor were many feces found there.

After arriving at a shelf, a mouse might stop in or at one or more boxes during its outward trip. Stops along a shelf outside of boxes were usually directly in front of a box or in the intervening spaces between boxes. There were normally fewer stops made during the return journay toward the ramp end of the shelf. During a continuous period of activity a mouse might visit each shelf one or more times before returning to the food pen or before entering a box for a period of rest. No pattern was ever detected of the order in which the four shelf levels on the right or left sides of the stand were visited.

One observation stands out in this description. This is that feces occurred in concentrations only at those places where the mice were observed to stop most frequently. In the discussion feces will be equated with the act of temporarily stopping, although adequate proof of the direct proportionality of defecation to stopping is lacking.

No mice were ever seen to transport nesting material. However, it was apparent that the mice occasionally removed nesting material from one box to an adjacent more distal one. Thus, the observed distribution of nesting material along the shelves showed a trend toward a more peripheral distribution than characterized the initial deposit by the mice.

Quantitative Observations

The total data for all colonies are presented in Figures 3 to 6 with respect to position along shelves or to the shelf levels. There was little justification for breaking down the data into that for each colony or into the several sub-samples of individual colonies. In general, all sub-samples were quite similar and no consistent change through time could be detected. In Figures 3 to 6 the abscissas are in terms of units of the equal distances between positions along shelves, or of the equal vertical distances between shelves.

The density functions of four items along the 1.2 meter shelves presented a pattern of a decreasing

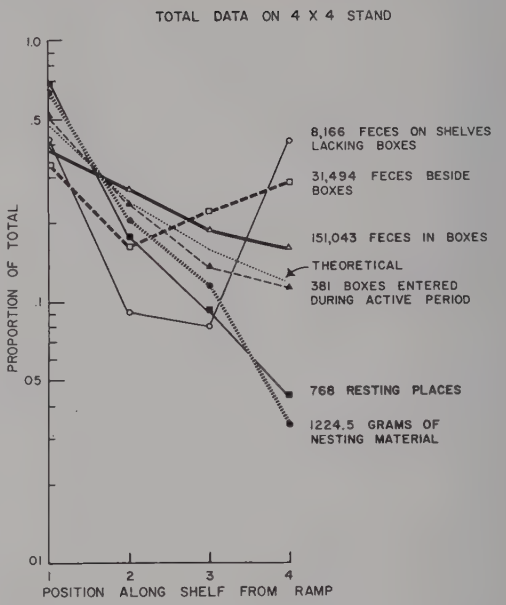

FIG. 3. The frequency of events along the shelves from the ramp. In all cases where the mice had to enter boxes the frequency of the item measured decreased as the distance from the ramp increased. The more goal-oriented responses, as reflected by resting places and transported nesting material, showed the most rapid decrease in frequency with distance. The more exploratory behavior, as indicated by feces in boxes or boxes entered, more closely approximated an inverse proportionality to distance. Where defecation occurred outside boxes there was marked peripheral increase. This increase is attributable to the end of the shelf acting as a barrier to outward locomotion when the environment was unstructured with nesting boxes, or when the mice were temporarily ignoring the boxes. There are fewer items in some categories than listed in Figure 4, since during the initial studies only the shelf level of some items was noted.

probability at locations increasingly distal from the point where the ramp joined the shelf (Fig. 3). These four items in the order of an increasingly lower probability at the more distant positions are: (a) feces in boxes; (b) boxes entered during periods of activity; (c) boxes in which the mice were observed resting; and (d) the amount of nesting material in boxes. One common property of these four events was that in each instance a mouse had to enter a box. However, there was a consistent minor deviation from the general trend of the data. This involved a slight increase in the most distal location, position 4, over that for position 3. Such an increase was recorded for eight of the twenty-eight sub-samples.

This increase in the probability of the event at the most distal location became pronounced for

the other two items recorded along the shelves. These two items, (a) feces beside boxes and (b) feces along shelves lacking boxes, possessed the common property of not entailing the entering of boxes by mice. In fact the probability of these two events at the terminal end of the shelf was nearly as great as at the initial position.

In contrast to the distribution of these six items along the shelves there were two main differences exhibited by their distribution over the four shelf levels (Fig. 4). Firstly, there was a higher probability of the items on the first shelf level than at the first box position, and there was a correspondingly more rapid rate of decline in the probability of the items from shelves 1 through 3 than for positions 1 to 3 along the shelves. Secondly, there was a marked increase in the frequency with which the items were observed on the fourth shelf level. The only exception to this was with reference to nesting material whose density function decreased so rapidly with increasing height that

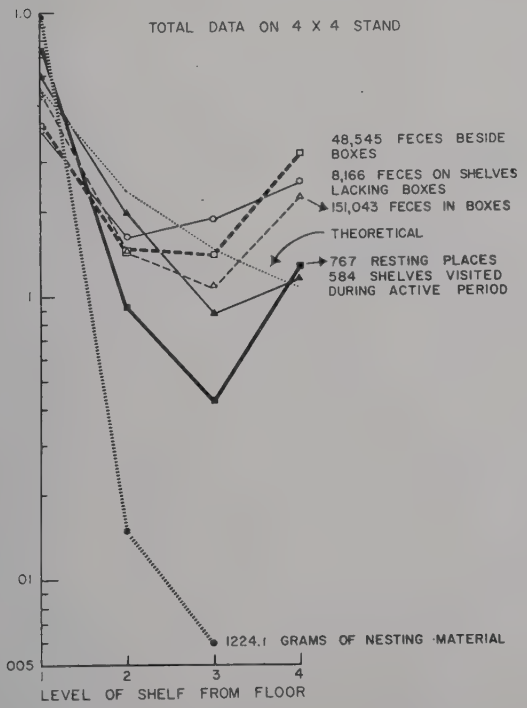

FIGURE 4. The frequency of events on shelves with reference to their distance above the floor. It may be noted that the differences in rate of decrease in frequency with increasing distance for the six measured items are in approximately the same order as they were along the shelves. The increase in frequency on the fourth shelf of most of the items is attributable to the increased probability of the mice encountering the base of the ramp to the fourth shelf when they departed from the food pen.

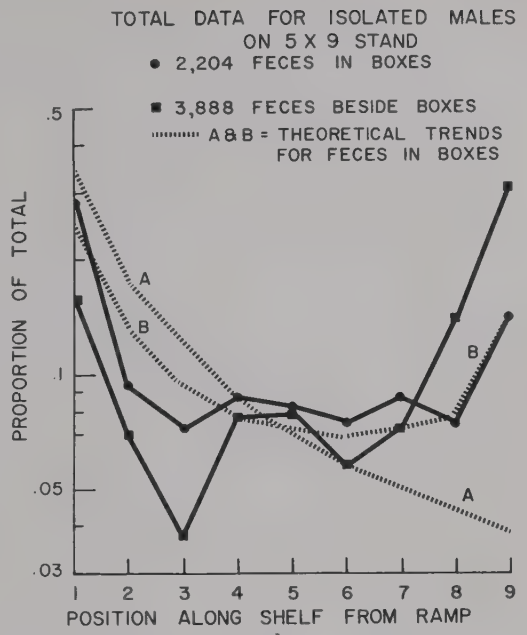

FIG. 5. The distribution of feces along shelves having 9 nesting boxes on each shelf. The increase in number of feces toward the terminal end of the shelf is accounted for by the fact that mice responded very little to the nesting boxes. This lack of response was due to the fact that each mouse had its own nesting box on the floor. Thus the mice behaved on these shelves as if they were relatively unstructured, and therefore, the mice frequently arrived at the terminal end of the shelf, which in turn served as a point of orientation. Theoretical trend A assumes inverse proportionality to distance when all orientations to the rest of the shelf originate from the ramp end. Theoretical trend B also assumes inverse proportionality to distance but with orientations initiated from both ends of the shelf.

no nesting material was ever recorded as having been transported to the highest shelf.

Only two items were measured on the stands having five shelf levels with nine boxes on each shelf. These two items were feces beside boxes and feces inside boxes (Figs. 5 and 6.) There was a characteristic U-shaped distribution of the density functions of each item, both along shelves and over the shelf levels. In other words, the probability of the items was greatest at both the near and far distances. Between these points there tended to be a decreasing probability such that the mid-distance had the lowest probability.

DISCUSSION

Distance as a Controlling Variable

The place where food, water, and nesting material were obtained served as a locus from which outward movements to the harborage stand usu-

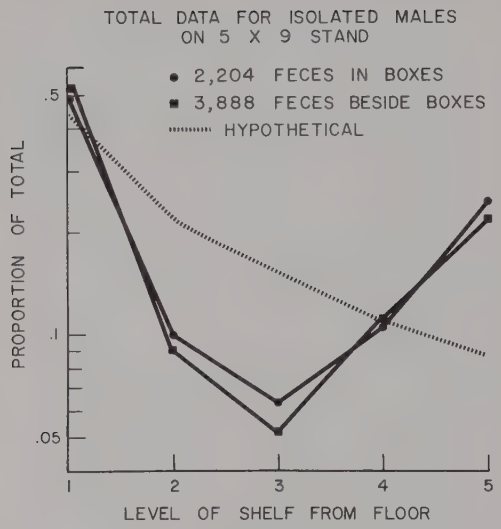

FIG. 6. The distribution of feces over the five shelf levels on the stand which had 9 nesting boxes on each shelf. This U-shaped distribution is particularly interesting. On the basis of a decreasing frequency with distance the decline from shelves 1 to 3 would be anticipated but not the increase from 3 to 5. The observed distribution appears to be related to the habit of the mice in running around the room adjacent to its walls. Ramp 5 would be encountered with nearly equal frequency to ramp 1, and likewise ramp 4 nearly as frequently as ramp 2.

ally emanated. However, it soon became apparent that one could not consider the food pen as the point from which distance to other points was to be measured when frequency of visiting these points is considered. For example, on shelf 4 the first box held four times as many feces as the fourth box (Table II). Yet in terms of equivalent horizontal distances from the food pen, the round trip distances to these two boxes must have been nearly the same, since the major expenditure of energy in reaching each of them included climbing the long, steep ramp to shelf 4. Therefore, if feces in the boxes were to be inversely proportional to these distances as measured in units of energy expenditure, box 1 on shelf 4 would have had only slightly more feces than box 4. Such discrepancies suggested that the distance from the food pen to the boxes was actually divided into three stages. First, there was the distance from the food pen to the bases of the ramps. This distance was ignored since the mice did not always approach the ramps from the food pen. Second, there was the trip up the ramp. Finally, once a mouse was on a shelf at the end of a ramp, it then could proceed along the shelf to a box. Selection of a particular ramp appeared to be a separate decision from choice of box to stop at before returning toward the ramp, even through these were consecutive responses. If this is so, and if visitations are approximately inversely proportional to distance, then the frequency of visitations at the four shelf levels will be inversely proportional to the relative vertical distances of the shelves from the floor. On these assumptions, the expected number of trips terminating on each shelf were calculated and are shown in Table I. Similarly, the expected number of trips terminating at each box position along the shelves was calculated as an inverse relation of the distance of each box from the ramp end of the shelf.

TABLE I. Expected proportion of visits at each of the sixteen positions on the stand provided that frequency of visitation is inversely proportional to relative distances.

Shelf	Vertical height from floor in inches	Expected proportion of total trips (A)	A x B			
4	68.5	.109	.052	.026	.018	.013
3	50.5	.148	.071	.036	.024	.018
2	32.5	.230	.110	.055	.037	.028
1	14.5	.514	.247	.123	.082	.062
Expected proportion of total trips (B)			.48	.24	.16	.12
Distance of entrance of box from ramp in inches			10.5	21	31.5	42
Position along shelf from ramp			1	2	3	4

The probability of an event occurring in any specific box should be the product of the probability of reaching that position along the shelf from the ramp and the probability of arriving at the particular shelf level from the floor (Table I). At least this will be true provided distance alone controls visitation frequency.

Many sets of data for the 16 positions indicated a general conformity to the hypothetical distribution, in the sense that density function decreased with distance. An example of one of the better approximations is shown in Table II. Since going up ramps and going along shelves were assumed to represent independent behaviors, the marginal totals for feces at the four shelf levels, and for feces at the four box positions were independently tested by Chi Square against the expected numbers. Both tests revealed a highly significant difference of the observed from the expected. It is therefore concluded that inverse proportionality to distance is an inadequate assumption of the usual monotonic decrease of density function with distance. In another study (Calhoun 1955) that evolved from the present one it was found that explorations by domestic rats from a nest box in a long narrow unstructured alley more nearly ap-

TABLE II. Example of the distribution of events over the harborage stand. 15,965 feces in boxes, DBA/2 Colony 1, 123 to 171 days of age.

Shelf		Box			
Level	Total	1	2	3	4
4	.089	.044	.019	.015	.011
3	.166	.073	.043	.029	.022
2	.266	.087	.078	.053	.047
1	.479	.133	.178	.091	.077
Total at box position:		.337	.318	.188	.157

proximated an exponential equation. Exactly what equations best describe movements from a locus of orientation must await further studies devoid of some of the complications of the present observations. However, differences in the rate of monotonic decrease in density of some of the observed behaviors, as well as certain marked exceptions from such a decrease, provide a basis for gaining insight into possible causes of this variability.

There is one marked difference between a mouse's choice of which ramp to take from the floor and its choice of a position along a shelf from the point where the ramp joins it. If a mouse makes the choice of going up a particular ramp and does proceed up it, it cannot arrive at another shelf without first returning to the floor. In contrast to this, if a mouse has arrived at a particular box it can go to another box on the same shelf without having to return to the ramp end of the shelf before exhibiting the second choice. These two ways in which the environment may be structured must result in quite different consequences in the way in which animals use space. A third situation, not treated in the present paper, is that presented by a plane surface in which diagonal movements are possible between neighboring routes of radial travel from a locus of orientation.

There were five separate responses reflected by the items measured on the harborage stands. These varied from the situation where a mouse merely roamed over the stand and only occasionally exhibited a simple response such as stopping and defecating, to that where, after going up from the floor, it went directly to a box and entered. The former may be designated as exploratory behavior and the latter as goal-oriented behavior. Exploratory behavior is here considered as the manifestation of the physiological drive to exhibit locomotor activity. In the present situation this was in large part expressed as movements away from and toward a center of orientation. During such periods of locomotion several responses to specific objects or situations were made, which appeared independent of other basic drives such as those of hunger, thirst, sex, or sleep. Such exploratory behavior takes place even in completely unstructured environments (Calhoun 1955). Defecation may be considered merely as a by-product of the act of stopping, since there was no evidence to indicate that excretions served as sign posts. Responses on the stand that are considered as components of exploratory behavior consisted in:

a. Stopping along shelf (and perhaps defecating) even when no boxes were on the shelf.
b. Stopping beside boxes (and perhaps defecating).
c. Entering boxes (and perhaps defecating).

Goal-oriented behavior involves the cessation of locomotion away from a center of orientation following the completion of a response which satisfies some need felt by the individual. Responses on the stand considered as goal-oriented behavior consist in:

a. Entering a box where a period of rest is initiated.
b. Entering a box and depositing a piece of nesting material.

There is probably a continuum of different categories of behavior lying between the extremes of exploratory behavior and of goal-oriented behavior. In goal-oriented behavior there is a tendency for the individual to return toward the center of orientation after having made a response. However, in exploratory behavior the probability is high that after making a response the individual will again continue away from the center of orientation.

Complexity of the Response

The only structures on the shelves of the harborage stand were the 150-mm-square wooden boxes. These elicited four responses: entering and depositing nesting material; entering and remaining for a period of rest and also possible defecating; entering temporarily and possibly defecating; and stopping beside boxes and possible defecating. The last two items were judged mainly through counts of deposited feces. These four kinds of behavior are listed in the presumed order of decreasing complexity. Complexity is considered as being determined by the number of motor responses and the energy expenditure involved. The respective proportions of the total records for each kind of behavior were: At the two most distal positions along the shelf: .164, .137, .347, .505. On the two uppermost shelves: .006, .170, .333, and .457. If this interpretation of complex-

ity of behavior is correct, there is only one exception to the generalization that the more complex the behavior, the smaller will be its density function at more distant points from a locus of orientation.

The one exception pertains to the increase in nesting material at the last two box positions over that of records of mice observed resting at these positions. This is simply accounted for by the fact that once nesting material was deposited in proximal boxes, it was later removed by the mice and transported to more distal locations along the shelves.

It will be noted that the probability of defecating in the two terminal box positions or in the boxes on the two upper shelves was twice or more that for records of mice resting in boxes at these positions. Thus, it is quite apparent that mice did enter boxes at these distal positions for purposes other than resting. This raises the question of why they entered the boxes in these distal positions when entering was not related to resting. The following interpretation is suggested: At the more proximal positions mice enter boxes and rest. They enter and rest more frequently at the proximal positions because this is a highly goal-oriented behavior, which is elicited among the first few appropriate objects encountered during outward travels from the food pens. Having entered boxes and rested at these proximal localities, the boxes assume the property of a reward. Thus during a portion of the time when exploratory visits were made to distal locations, enterings are elicited, although they less frequently terminate in the consummation of the behavior by cessation of activity.

These considerations have led to the following generalizations: The more goal-oriented a behavior becomes, the steeper will be the monotonic decrease of its density function curve with distance. The least goal-oriented behavior may be designated as exploratory behavior, and its density function curve should be characterized by the least rapid decrease with distance.

Density of Objects in the Environment

The least structured environment in this study was represented by the set of shelves available to DBA/2, Colony 2, and to C57BL/10, Colony 2, upon which there were no boxes. In this situation the feces were concentrated at either end of the shelves with relatively few over the central halves of the shelves (Fig. 3). The interpretation placed upon this distribution is that where there are no objects along a route from a point of orientation the density function of an event will have the lowest rate of decline associated with distance, because of the absence of stimuli eliciting those responses entailing stopping. However, the 1.2-meter shelves were so short that on any outward journey a mouse would nearly immediately find itself at the end of the shelf. Having been stopped by this barrier, defecation frequently ensued. The end of the shelf probably served as a secondary center of orientation from which movements were directed back toward the ramp end, where the mouse again might stop before returning down the ramp. This same rationale may account for the general observation that animals maintained in pens beat a path about the periphery.

Even where an environment is structured, the degree to which movement away from a center of orientation is inhibited depends upon the particular responses made by the mouse. For example, consider the events of defecation on shelves structured by boxes (Fig. 3). Despite considerable increase in defecation beside distal boxes, the fact that there was more defecation over the central half of the shelf than characterized shelves lacking boxes, indicates an inhibition of motion by a structured environment. Defecation beside boxes is presumed to result from a type of exploratory behavior independent of that which involves entering boxes. The reason for believing this is that the density function of defecation beside boxes is quite different from that within boxes. Furthermore when a single box was selected by a group of mice as a place where they went for periods of rest, the amount of feces in it showed a marked increase over neighboring boxes, but there was never a corresponding increase in the feces beside boxes. Also, mice were sometimes observed to roam over the shelves and enter nearly every box, but they rarely stopped beside boxes. Conversely, during periods of roaming over shelves mice frequently stopped beside boxes, and yet rarely entered boxes. Although this may argue for the discreteness of the more complex response involving entering a box, it did not preclude the interspersion of both events during a period of exploration. Even so the probability of the more complex behavior of entering a box before defecating did show a more marked decrease with distance than did the simpler behavior of defecating beside boxes.

The Density Function along 2.75-meter Shelves

As a result of the data summarized in Figure 3 for the 1.2-meter-long shelves, it was anticipated that, were a longer shelf made available to the mice, there would result a gradually declining density function with distance even for such an item as feces beside boxes. The reason for this anticipation was that there should be less opportunity

for the "piling-up" effect produced by mice arriving at the terminus of their environment. Actually this proved not to be the case as may be seen from Figure 5. Instead of obtaining a curve of monotonic decrease with distance, a distribution resulted in which the largest number of feces were at either end of the shelf, with a decline from either end toward the middle.

There appears to be a relatively simple explanation for this distribution. One assumption is requisite. This is that nesting boxes along the shelves served as a very weak stimulus in eliciting stopping or entering responses. Reasons for this assumption will be given below. Assuming the correctness of this assumption, what would be the behavior of mice on the shelves? Let us first consider only those trips which terminated at some point along the shelf proximal to its terminus. Continuously fewer trips will terminate at increasing distances from the ramp. Each such trip may be characterized by one or more stops in either direction. The end result of these trips is a monotonic decrease in stops with reference to the ramp end of the shelf. However, in addition to such trips, the mice frequently arrive at the terminal end of the shelf without stopping, because the nest boxes serve as a weak stimulus for these mice. Once at the end of the shelf the mice return toward the ramp after a short stop. Stops may be made along the way. One would anticipate that each stop reduces the motivation to stop, once travel toward the ramp is resumed. Such trips from the terminal end will result in a monotonic decrease in stopping as the ramp is approached. Stopping (and defecating, or entering boxes and defecating) will relate to two monotonic decreasing distributions, one beginning at either end of the shelf. If these two are summated, a U-shaped distribution results. I have assumed that the number of feces at the 1st and 9th position are roughly proportioned to trips started from either end of the shelf. If frequency of stopping and defecating is inversely proportional to distance, an expected number of stops in either direction at each of the nine positions may be calculated. This was done and the two distributions were summated (Curve B, Fig. 5). This curve roughly approximates the observed data. The error mainly lies in the assumption of inverse proportionality to distance. An assumption of exponential decrease with distance would have given a better approximation.

There is one peculiarity of the observed data for which I can only hazard a tenuous guess. No assumption of monotonic decrease will account for the excess of feces over the central portion of the shelf. It will be recalled that the nest cages on the floor into which the mice retired were directly under the center of the stand. Mice on the floor did approach these nest cages from the direction of the braces at either end of the stand. If the act of stopping in the nest cage after traversing this distance was actually rewarding, one might anticipate a tendency to stop on the shelves above after having traversed a similar distance from either end.

Whether the mice were run singly or in groups, they almost invariably returned to their cages on the floor during periods of rest. That the boxes on the 5 x 9 stands actually did not hold such an attraction for the mice as on the 4 x 4 stands is revealed by the following: For DBAs on the 5 x 9 stand in groups there were only 10 feces per mouse per day in boxes, whereas for the most nearly comparable measurements on the 4 x 4 stand there were 55 feces per mouse per day in boxes. Similarly, for the C57 mice in groups on the 5 x 9 stand, there were only 18 feces per mouse per day deposited in boxes, whereas for the most comparable data on the 4 x 4 stand, there were 41 feces per mouse per day in boxes. For the isolated mice on the 5 x 9 stand, the feces per day per mouse was 8.8 for DBA's and 3.6 for C57's. Another indication of the difference in responding to boxes may be gained by comparing the data in Figures 4 and 6 for feces in and beside boxes. On the 4 x 4 stand there were only .32 feces beside boxes for every one in boxes, while on the 5 x 5 stand there were 1.76 feces beside boxes for every one in boxes. In other words the boxes on the 5 x 5 stand held only about 18 per cent of the attraction for the mice that they did on the 4 x 4 stand. These data indicate that the shelves on the 5 x 9 stand were quite unstructured in so far as eliciting responses by the mice were concerned, in contrast to the more frequent responses elicited even during exploratory behavior on the 4 x 4 stand where such boxes were the only places available for retiring during resting periods. The act of entering a box on one of the lower shelves of the 4 x 4 stand for the purpose of resting represented a highly goal-oriented response, that is the response was rewarded or reinforced. As a result there was generalization of the stimulus (the box) at its other locations where the mice rarely rested (Fig. 4), and thus wherever a box was encountered it was more likely to elicit the response of entering. However, the effect of this generalization declined with distance from the first shelf where entering was more frequently rewarding. Thus the number of feces beside boxes for each one in boxes from shelves 1 to 4 were respectively

.25, .32, .38, .45 (derived from data in Fig. 4). For the mice exploring the 5 x 9 stands, the act of entering a box even on the lowest shelf was rarely rewarded, since reward was associated with response to a differentially structured cage on the floor in which they had been living for several weeks prior to placing it and the mouse in the pen. Therefore, there arose an increase in density function toward the distal end of the 2.75-meter shelves since with respect to the motivation of the mice these shelves were relatively unstructured. Furthermore, these distal locations then assumed the character of a locus of orientation.

The Direction of Movement

Responses to objects along the route of travel are more likely to be made while moving away from a center of orientation. This is an hypothesis based mostly upon unrecorded recollections. However, one set of data supports this belief. All the details were recorded for 41 round trips from the ramp end of 1.2-m-long shelves. Of 155 boxes reached on outward trips, 80 were entered and 75 passed. On the return trips, of 103 boxes reached only 13 were entered. Furthermore, there were additional data upon 28 boxes which mice entered and in which they remained. Every such instance of entering and remaining occured while a mouse was on an outward journey.

Probability of Contacting a Ramp versus Motivation

With every item measured, except deposition of nesting material, there was a marked increase in the density function on the fourth shelf level (Fig. 4). The previous account of the behavior of the mice in approaching the ramps is pertinent. This indicated that the approach was usually directly from the entrance to the food pen or from underneath the central portion of the stand. In the former case, the mice would first encounter the base of the ramp to the fourth and highest shelf level. In the second case, the first ramp to be encountered was that to the lowest shelf level (Fig. 2). Ramps to the second and third shelf levels would be encountered only after having previously encountered one of the other two. Another relevant aspect of the situation was that it was an extremely rare event for a mouse to turn around once it had started up a ramp. It is therefore concluded that the increased frequency of events on the highest shelf depended upon an increased probability of encountering the ramp to the highest shelf, coupled with the fact that once initiated, the journey up the ramp was generally completed.

Another point was that items reflecting exploratory behavior had a higher probability on the top shelf than those reflecting goal-oriented behavior. If we consider events observed on the top shelf (Fig. 4), we find that both the items measuring feces outside boxes had the greatest probability; feces in boxes a smaller probability; resting and the visitation of shelves had still lower probabilities; whereas the entirely goal-oriented behavior of depositing nesting material not only failed to show an increase in probability for the third to the top shelf, but no nesting material at all was found there.

This must mean that the greater the motivation to enter a box at the time the mouse leaves the food pen, the more likely it is that the ramps to the higher shelves will be ignored. That the mice do ignore the bases of the ramps to the higher shelves under such circumstances, indicates that they are actually aware of the relative distances involved. Furthermore, the lessened influence of distance on more exploratory types of behavior indicates that a reduced motivation of orientation toward a goal reduces the likelihod of distance discrimination.

In one particular situation the boxes on the uppermost shelves developed the character of a reward for certain mice. Social hierarchies developed among males. A subordinate male was more likely to escape pursuit from a superior if it ran to a higher shelf. For example, in DBA/2, Colony 1A, the frequency with which mice were found resting in boxes on shelves 1 to 4 were: (a) .859, .120, .014, and .007 for 142 records of the three females; (b) .763, .198, .013, and .026 for 76 records of the two higher ranking males; and (c) .356, .222, .178, and .245 for the 45 records of the low ranking male. This influence of social rank is discussed in more detail in another paper (Calhoun 1956). Although low social rank did influence the increase in the probability of events on the fourth shelf, it is believed that the main determining factor was the increased probability of mice contacting the base of the ramp to the fourth shelf.

More precise insight into this problem of the influence of the probability of initiating a response upon its completion may be gained from an examination of the data relative to isolated males exposed to the harborage stand having five shelf levels (Fig. 6). Since the mice were run alone in separate trials, there was no possibility of the results having been complicated by the social structure of the group. Also the situation was uncomplicated by goal-oriented behavior, since the mice infrequently used the boxes on the stands for either resting or building nests, but instead

returned to their cages on the floor where food, water, and a nest had been supplied them. Thus most visits to the stand represented exploratory behavior. From this cage on the floor the bases of all 5 ramps were nearly equidistant, with a slightly shorter distance to the ramps of shelves 3, 2 and 4. For this reason, the position of the harborage cage may be eliminated as a major variable in producing a differential probability of encountering the bases of the ramps.

However, there was one important aspect of the physical structure of the environment as well as one important behavior which must be considered. The bases of the 5 ramps lay in a line close to the wall. The ramp to the lowest shelf was at one end of the line and the ramp to the highest shelf was at the other end. The mice spent a great deal of time circling the floor of the pen in close proximity to its walls, and during the circling they would come into contact with a ramp and proceed up to the shelf to which it led. In such movements the ramp to shelf one or that to shelf five would be encountered first. In order to encounter the ramps of shelves two and four, the mouse had to by-pass the ramp to either shelf one or five without responding to it. Regardless of which direction the mouse was going, it had to by-pass the bases of two other ramps in order to arrive at the ramp to shelf three.

It has, therefore, been concluded that it was this differential probability of encountering the ramps which produced a "U-shaped" density function rather than one of decreasing probability at greater distances (Fig. 6). There was no systematic difference between the distribution of feces in boxes and beside boxes. Groups of mice exhibited the same general pattern except that there was an even more pronounced concentration of feces on the upper levels.

Movement in Relation to Size of Animal

No systematic differences were observed between the utilization of the harborage stand by DBA mice and by C57 mice. These two strains were essentially identical in size, the adults weighed approximately 27 grams. However, there were two strains of mice available at the Roscoe B. Jackson Memorial Laboratory which varied markedly in size. The Small mice attained less than half the adult weight of the larger more obese Large strain. Each of these strains exhibited density functions of recorded items which were quite similar to those for DBA and C57 mice. However, the frequency with which defecation occurred on the stand differed markedly. There was an average of 1798 feces per Small strain mouse for the duration of the study but only 609 for each Large strain mouse. This difference conforms to the observed behavior of the mice. The Small mice not only spent a great deal of time roaming over the stand, but they also spent their resting periods in the nesting boxes on the stand. In contrast to this, the Large mice huddled in groups on the floor of the pen, either in the food pen or in the corner of the main pen, and only occasionally ventured up on the stand. Qualitative observations showed a much greater concentration of feces on the floor for the Large mice. From these observations the following inference is tentatively drawn: When the physiology or morphology of an individual is such that relatively more of its available energy is required to traverse a unit of distance, the frequency with which it makes excursions to and from a locus of orientation will be reduced, but the form of the density function will be unaltered. That is any two points in the environment will be visited less frequently, but the number of visits to one of the points remains the same relative to the visits to the other.

Summary

Colonies of inbred strains of house mice were established in standardized environments in a large room. Each standardized environment consisted of a pen covering 9.75 sq. meters of floor space. In each pen there was a harborage stand and a smaller pen. The smaller pen, which had a single route of access from the larger pen, contained hoppers for food, water, and nesting material. On the harborage stand there were eight shelves, two at each of four levels from the floor. Four nest boxes were equally spaced along each shelf. A ramp connected one end of each shelf with the floor. The bases of these ramps formed a group of points near the center of the pen. All the nest boxes were removed from the left hand set of shelves in the pens in which the members of two colonies lived. Another alteration to the harborage stand used in one group of studies was that it consisted of five longer shelves, one at each of five levels from the floor, upon each of which were nine equally spaced nest boxes. In this latter group of studies there were also two conditions which differed from all the other studies. (1) Accessory nesting boxes in which the mice had previously been living and which were differently shaped than those on the shelves were placed on the floor under the harborage stand. (2) The bases of the five ramps lay in a line adjacent to the wall of the pen. Observations were then made of the positions in these environments to which the mice went, or at which specific behaviors were elicited or terminated. Counts were made of the position of mice, their feces, and transported nesting mate-

rial. Locations of these items were expressed in terms of (1) the relative vertical heights of the shelves from the floor (2) the relative distance along the shelf from the end where the ramp joined it or (3) the probability of encountering the base of a ramp.

A. There were three general observations:
   1. Mice rarely stopped on the unstructured floor of the pens.
   2. Movement on the floor was primarily from the food pen door to the bases of the ramps, around the periphery of the pen, or toward the portion of the floor shaded by the overhanging lowest shelf.
   3. Stopping on the floor was primarily confined to contact with the wall, particularly at the corners of the pen or adjacent to the braces supporting the harborage stand.

B. The following observations concern the harborage stands having shelves at four levels:
   1. In general items were noted most frequently on the lowest shelf and at the box on each nearest the ramp, and continually fewer items were noted at each successive greater distance, whether measured vertically or horizontally.
   2. Items judged as components of exploratory behavior, such as temporary stopping, with or without defecation, were noted more frequently at more distant points than were other items such as entering boxes to rest or to deposit nesting material, which were judged as goal-oriented behavior.
   3. On shelves lacking boxes feces were noted as frequently at the terminal end of the shelf as on the end adjacent to the ramp. Very few were located over the central half of the shelf.
   4. The item judged as most characteristic of exploratory behavior (*i.e.,* feces outside of nest boxes) was noted more frequently on the highest shelf level than on the next two lower shelves. This is related to the observation that a mouse departing from the food pen usually encountered the ramp to this shelf before it did the others. In contrast, items characteristic of goal-oriented behavior (*i.e.,* deposition of nesting material) were never even observed on the highest shelves.

C. The following observations concern the harborage stand on which there were shelves at five levels:
   1. Items such as entering a box to rest or to deposit nesting material, which reflect goal-oriented behavior, were rare on these stands.
   2. Feces in or beside boxes were most frequent at the two ends of each shelf. The number of feces declined from either end toward the center.
   3. The most feces were found on the lowest and on the highest shelves, while the fewest feces were found on the middle of the five shelves. This is related to the observation that mice running around the pen against the wall encountered ramps to shelves one and five with nearly equal frequency; and that ramps to two other shelves had to be passed before encountering the ramp to the middle shelf.
   4. Per unit of time these mice, who had accessory but different type nest boxes on the floor, explored the upper four shelves of the harborage stand much less frequently than those mice living in boxes on the first shelf level of the stands with four shelf levels explored the upper three levels on their stands.

These observations suggest the following interpretations:

1. Probability of stopping is low in unstructured space. (Obs.: A-1, A-3, B-3)
2. The basic relationship between distance and the probability of arriving at a point and stopping at it is that there is a monotonic decrease, with increasing distance. (Obs.: B-1)
3. The more goal-oriented is a response the greater will be the monotonic decrease with distance. (Obs.: B-2)
4. Where the distance intervening between a point of orientation and the terminus of the route is relatively short, the terminus serves as a barrier at which stopping is frequent (Obs.: B-3)
5. When mice are highly motivated they select the shortest route to a goal. (Obs.: B-4)
6. When mice are not highly motivated the route of travel is primarily determined by the probability of encountering the origin of the route, irrespective of its distance. (Obs.: B-4, C-3, C-4)
7. When responses to objects in the environment are infrequently rewarded (reinforced), spatial orientations are as if these objects were not present. (Obs.: C-4, compare C-2 to B-3)

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PLANT SUCCESSION ON A SUBALPINE EARTHFLOW IN COLORADO

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The opportunity to study initial stages of plant succession upon bare areas has been of considerable interest to plant ecologists. Successional patterns have been investigated in many regions, and in some cases it has been possible to date the baring of the surface and to follow consequent vegetational changes over a period of years. Studies of this sort have been carried out on glaciated areas (Cooper 1923 a, b, c, 1931, 1939), coal stripped lands (Croxton 1928), sand bars (Lakela 1939), abandoned crop lands (Johnson 1945), sand flats (McVaugh 1947), volcanic areas (Eggler 1948), *et al.* Study of the revegetation of areas disturbed by various forms of mass movement, however, seem to have been neglected. These phenomena are also of practical interest because of extensive damage to agricultural and grazing land, mining activities, and to communication lines in some parts of the country. In some areas, they have endangered life by damming streams and flooding the surrounding countryside. The ecologist as well as the geomorphologist can contribute valuable information regarding their prevention and control (Ellison and Coaldrake 1954).

This paper presents the results of a study of the causes, nature, and date of occurrence of an earthflow, and the successional patterns in the revegetation of it. This earthflow occurred in East River Valley near the old mining ghost-town of Gothic in the Elk Range of Colorado. The Elk Range lies in central Colorado west of the Continental Divide. It is separated from the White River Plateau on the north by the synclinal valley of the Roaring Fork River, and the Sawatch Range adjoins it immediately to the east. The valley of the Gunnison River separates it from the San Juan Mountains on the south, and the mesa country of Colorado extends westward (Fig. 1). The range is high, having many peaks with elevations of 13,000 to 14,000 feet. Glacial and stream erosion of steeply tilted sedimentary rocks and included sills, stocks and laccoliths have produced a characteristically rugged topography, with numerous cirques, glacial lakes, U-shaped valleys, and extensive moraines. Topographic and lithologic conditions are particularly favorable for the development of such mass earth movements as landslides, talus slides, earthflows, and rock streams.

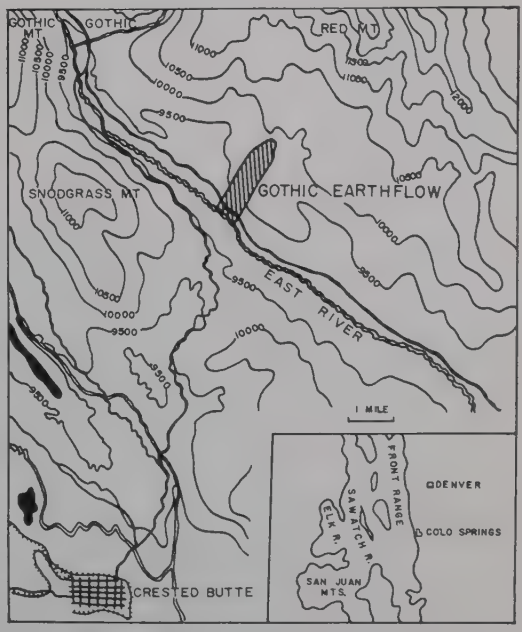

Fig. 1. Index map of Colorado showing the location of the Elk Mountains and topographic map of the Gothic area showing the location of the Gothic Earthflow. Topography from U.S.G.S., Crested Butte quadrangle, Colorado.

East River Valley occupies a major syncline which lies west of the anticlinorium making up the Elk Range. It is a typical U-shaped glacial trough carved by the East River and Copper Creek glaciers. East River, which now occupies the valley, flows southeastward along the former glacial path. In places, it passes through moraines in steep narrow gorges, but elsewhere it flows with wide sweeps across a broad valley floor in a well-developed meander pattern. The elevation of the valley floor varies from 9,000 to 9,600 feet. Lateral moraines occur on both sides of the valley at elevations as high as 10,500 and 11,000 feet. A series of rock terraces veneered with moraine, and numerous end moraines are also prominent features. Some of the terraces have been modified by mass movement, and many of the moraines are deeply gullied by small tributary streams working headward. Terracettes produced by creeping of the surface layers are also extensive.

It is a pleasure to acknowledge the assistance of numerous individuals which made possible the completion of the study. William S. Cooper offered valuable criticism throughout the project. Harriet G. Barclay, A. O. Weese, and Clifford Chappel assisted with field activities during the summer of 1936. Ralph L. Langenheim, Jr., assisted with mapping the flow and in establishing permanent quadrats. Robert P. Sharp and H. E. Wright gave advice concerning the physiographic conditions. Herbert L. Mason and Helen K. Sharsmith critically read the manuscript offering numerous helpful suggestions concerning content and expression.

Physiography

Classification of mass movements

Many schemes for the classification of mass movements have been suggested. In a thorough review of the subject, Sharpe (1938) established a comprehensive and useful system of classification resting upon three sets of variables: 1) type of movement—whether flow or slip, 2) relative rate of movement, 3) relative proportions of water, ice, earth, or rock.

The Gothic Earthflow represents compound movement which involved both flowage and slippage in the same earth disturbance, thus meeting Sharpe's criteria for classification as an earthflow with an associated slump block. Sharpe considers the earthflow to be a product of flowage of earth or rock sufficiently saturated with water for the movement to be perceptible. Relative rapidity of movement is directly dependent upon the type of substratum, its degree of saturation and consequent internal lubrication of the matrix, steepness of slope, and the amount of stabilizing vegetation cover. An earthflow is distinguished from a mudflow by virtue of the more fluid behavior of the latter.

The term slump is associated with a downward slipping of a mass of substratum moving as a unit or several subsidiary units. The slip surface forms a deep-seated spoon-shaped basin, and thus the moving mass usually rotates backward on a more or less horizontal axis parallel to the cliffs from which it descends. Slumping generally requires removal of support from beneath the toe of the slump block. This results where rivers or

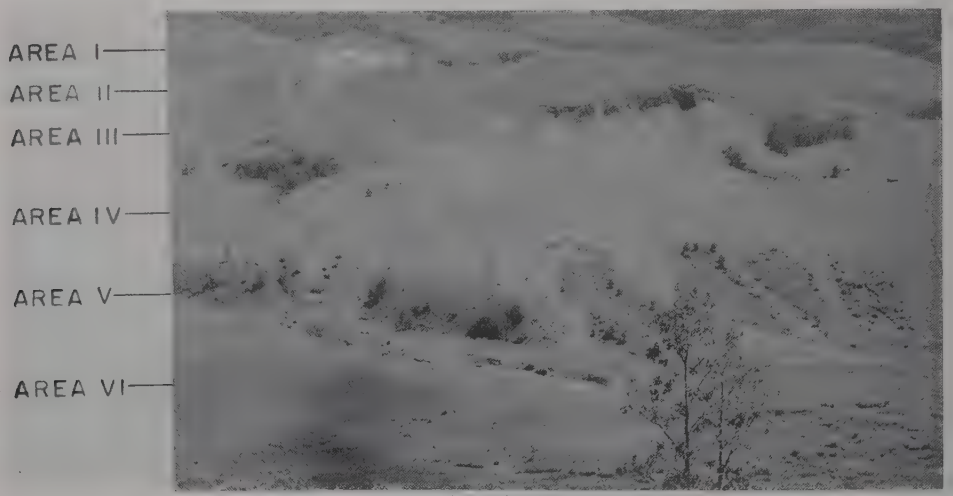

Fig. 2. The Gothic Earthflow from the Gothic-Crested Butte road.

waves undercut banks or where material lower down the slope is removed by an earthflow. Most slumps move slowly and intermittently over a long period of time, but some are completed in one rapid slip.

Descritpion of the Gothic Earthflow

The Gothic Earthflow is located in Sec. 11, T. 13 S., R. 86 W., Gunnison County, Colorado. It is a prominent landscape feature observable three miles south of Gothic from the road to Crested Butte (Figs. 1 and 2). A contour map was made of it by plane table and alidade (Fig. 3). The flow is approximately one mile long and one-quarter mile wide. The elevation is approximately 9,950 feet at the head break and 9,200 feet at the foot of the debris. In general exposure, it faces southwest.

To facilitate reference, the flow is here classified into six major areas, this division being based upon general physiographic conditions significant to, and reflected in, the character of the vegetation. A brief description of each is given below:

Area I.—Upper break-away scarp. This is a V-shaped scarp, exposing 30 to 40 feet of moraine overlying strata of indurated shale. The lower portions of the slope are covered by a relatively stable talus of glacial debris and soil.

Area II.—Slump block. This area is characterized by gently rolling morainal topography; it was essentially unaltered by movement, because the block slumped as a unit.

Area III.—Lower break-away scarp. Two types of movement occurred along this scarp. In the eastern portion flowage produced a slope of 36° on which shale fragments are still in continual movement. A prominent ledge of indurated shale caps the scarp here. Along the western portion of the scarp there is no evidence of flowage of shale. Instead, the relatively stable slope is characterized by islands of vegetation which have slumped essentially intact.

Area IV.—Main body of the earthflow. This is the largest section of the flow; it is relatively stable with slopes ranging from 6 to 8°. It has the general appearance of a dump ground with large blocks of indurated shale scattered along the flow pattern of the shale particles. Boulders of diverse lithology from the moraine, and slump islands of soil are also interspersed, but occur less prominently.

Area V.—Slope descending to valley floor. Tongues of shaly debris with intervening undisturbed areas characterize this slope which has a gradient ranging from 15 to 20°. Deep drainage channels have been cut into the debris tongues by meltwater, leaving high current levees on both sides of the channel.

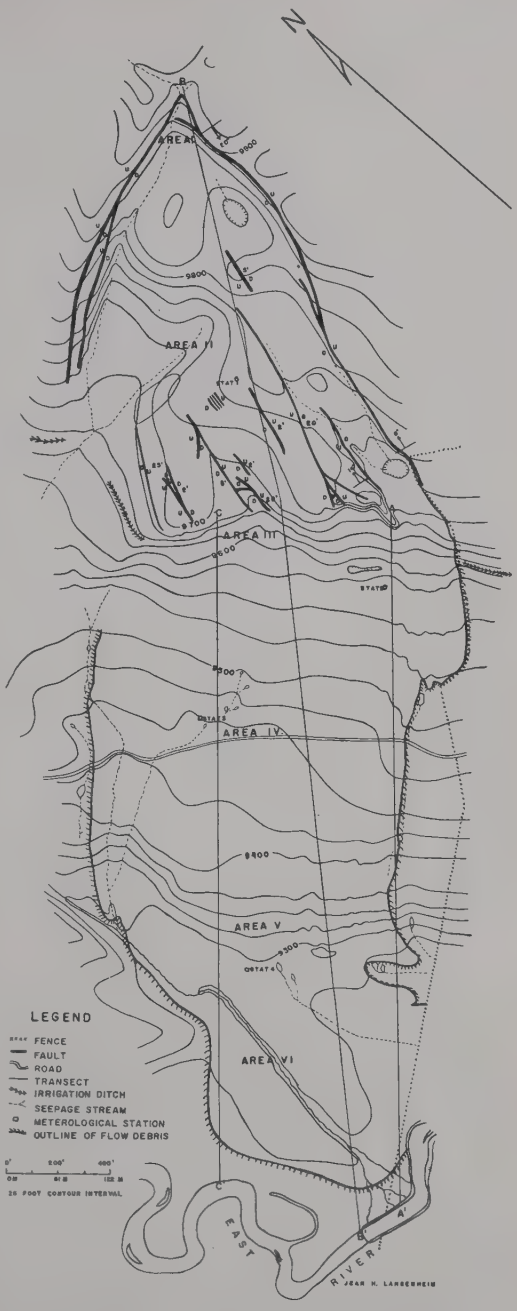

FIG. 3. Topographic map of the Gothic Earthflow.

Area VI.—Valley floor. This area constitutes the flood plain of East River. Shale particles, washed from the snouts of the debris tongues, veneer por-

tions of the valley floor, although most of the area has remained unaffected.

Causes of the Gothic Earthflow

The Gothic Earthflow and associated slump block occurred as a result of saturation of the substratum by water in combination with topographic, stratigraphic, and structural conditions particularly favorable for movement. First, the location on a relatively steep, terraced slope provided a suitable topographic situation. Secondly, the stratigraphy of the mass, together with the lithology of the various beds, provided optimum conditions for movement. The morainal mantle, 30 to 40 feet thick at the upper break-away and only 2 to 3 feet thick in Area III, allowed easy penetration of water. The Pierre shale, next below, is laminated and friable. It weathers rapidly, and when well-lubricated provides an excellent flow matrix. This shale is jointed and fractured permitting water to penetrate the rocks below. A thin impermeable layer of brick clay is reported beneath the shale which, by trapping water, could contribute to saturation of the mass above. Underlying the brick clay, although not exposed on the earthflow, is 100 to 200 feet of massive Niobrara limestone. Its fractured condition and comparatively high solubility promote action of ground water, which may or may not have directly influenced the flow. Third, the slump block of Area II was located in a minor fold on the eastern limb of a larger syncline, and thus bedding plane surfaces were parallel to the slip surface and facilitated movement. This feature also probably accounted for the movement of the slump block as a unit.

In addition to heavy precipitation characteristic of the area, an irrigation ditch, underground water, and a reservoir provided possible sources of water that may have produced saturation sufficient to have initiated movement. The irrigation ditch crosses the site of the lower break-away escarpment. Numerous leaks are reported to have occurred in this ditch, which undoubtedly produced local areas of saturated substratum. No permanent streams pass directly over the flow nor are there any evidences of former courses. Many small streams originating in névé patches on Red Mountain, however, come down the slopes above the flow. The majority of these sink into the ground at 11,000 to 10,500 feet, but often reappear in aspen groves as seepage. Seepage areas occur on the flow, and are most conspicuous where there is a heavy covering of debris. Seepage zones could have provided another means by which the substratum became saturated. Miners and ranchers state that a small lake just above the flow, now indicated only by a large depression, was utilized as a reservoir. Water from this reservoir would, of course, have been an additional source producing saturation.

Nature of the movement

Opinion among local residents is unanimous that there were no major breaks in the landscape previous to the apparently sudden occurrence of the flow. The present major surface features, and the area they occupy, seem also to have resulted essentially from this initial movement. The only continuing movement since the original flow has been that of surficial material, which is particularly evident on the steeper slopes and probably results from the action of spring melting of heavy snowfall, frost, and torrential rains plus the activities of burrowing animals such as marmots and pocket gophers. There is photographic evidence that at least since 1928 no major movement has occurred, for a photograph of the flow taken that year is very similar to photographs taken in 1948 and 1950.

There appear to be two sites where movement could have started, but evidence does not permit a choice between them. One possibility is that movement was initiated in the region of slump (Areas I and II) through a combination of favorable structural conditions and seepage from the reservoir. As the block of ground slumped forward, the addition of its weight could have started the flow of the lower part in the area saturated by the irrigation ditch. The other possibility is that the flow of the lower part, resulting from the saturation of the substratum by leaks in the irrigation ditch, took place first. The consequent removal of support then would have brought about the slumping of the upper areas.

Date of occurrence

The date of occurrence may be closely approximated by mutually corroborative evidence from three sources—local information, climatic data, and tree-ring analysis. The estimates of ranchers and miners, familiar with the area for most of their lives, ranged from 1920 to 1925. Unfortunately no record of the event was published in the Gunnison newspaper, and the owner of the property no longer resides in the area. However, Dr. John C. Johnson, Director of the Rocky Mountain Biological Laboratory, took classes to the area during the period 1920-1925. He first noted the flow in the spring of 1923.

Weather Bureau records from Crested Butte give circumstantial evidence supporting this date. The total of 20.77 inches of winter precipitation in 1922-23 is the highest recorded during the

period 1910 to 1930—the average winter precipitation being 11.11 inches. Accumulation of moisture through several years of average precipitation with winter precipitation increasing to a climax in 1922-23, might well have initiated movement in 1923.

The most satisfactory evidence pointing toward 1923 is the record which occurs in the trees bordering the flow. Any disturbance causing bending of the trunk will be recorded by the initiation of eccentric development of annual growth layers. The number of these eccentric layers serves to date the disturbance. Groves of aspen on the southeast and northwest margins of the flow were sideswiped by debris, as shown by trees which still have shale piled around their bases. In the summer of 1947 the debris was removed as thoroughly as possible from several of these, and the trees cut down. Two-inch sections from near the base were cut and polished. Twenty-five eccentric layers were found in each case, indicating that the distortion of the trunks occurred in the spring of 1923 before initiation of wood formation. Trees not touched by debris were cut to serve as controls. All growth layers in these were concentric.

Environmental Conditions on the Earthflow

Climatic conditions

There are no adequate climatic data for the area in which the earthflow is located. The nearest Weather Bureau station is at Crested Butte, about 5 miles southeast at an elevation of 8,867 feet. Here the 41-year record shows an average annual precipitation of 28 inches (U. S. Dept. Agric. Yearbook 1941, U. S. Dept. Commerce, Annual Climatic Summary, 1952), and it has been assumed that precipitation is probably higher at the higher elevations of the earthflow. There are two maxima of precipitation, one occurring through the period July to September and the other in January. June and October are usually periods of drought. The summer precipitation results from periodic cyclonic storms combined with daily, convectionally produced showers. Snowfall is exceptionally heavy, and persistent accumulations at higher elevations in the Gothic area provide a source of moisture throughout the summer.

At Crested Butte, the mean temperature for July is 56.6° F. and for January, 12.6° F.; the absolute maximum temperature on record is 91° F. and the absolute minimum is —42° F. The average date for the last killing frost in the spring is July 2, and August 22 is the first for the fall. Thus, the apparent frost-free season is 51 days at Crested Butte. At Gothic, at an elevation of 1,000 feet higher, however, frosts are known to occur occasionally throughout the summer.

To substantiate the assumption that more precipitation is probably received on the earthflow than in Crested Butte, four stations were established on the flow in the summer of 1946 to record precipitation for the period July 9 to August 20. Evaporation rates were also recorded by Livingston porous clay atmometers. Locations were selected to represent either observable differences in the mosaic patterns of species populations or possible extremes produced by exposure or topography. Because no significant differences appeared in the precipitation and evaporation totals between the stations, averages for all stations can be taken as a picture of conditions on the earthflow as a whole. For the six weeks' period, the precipitation total was approximately 5.52 inches; the evaporation total was 1254.8 cc. There was considerable variation in the amount of precipitation received each week, ranging from 0.38 to 1.52 inches; the evaporation ranged from 109.7 to 308.5 cc., in every instance varying inversely with the precipitation. The precipitational maxima could be correlated with the occurrence of cyclonic storms. The Weather Bureau records for Crested Butte showed an average precipitation total of only 4.54 inches for the months of July and August, a period two weeks longer than that during which the records were kept on the flow. These data are indicative of a possible difference in summer precipitation between the two areas but are not conclusive evidence in a region with so much convectional precipitation.

Edaphic conditions

The substrata on the earthflow vary from bare shaly parent material to well-developed soil. Since the vegetation will be discussed by areas, there follows a characterization of the edaphic conditions for each of these areas. The substratum, in those parts of Area I which suport vegetation is a talus composed of glacial debris and soil material. It has the character of sandy loam; rocks, varying in size from pebbles to boulders, are scattered over it. The talus is relatively stable, as movement downhill farther than the scarp exposure is prevented by the slumpblock comprising Area II.

Area II is a dislocated portion of the original slope, on which the substratum is barely disturbed. Sections observed in numerous localities here indicate that the soil is relatively uniform and has been developed on moraine. A typical profile is as follows: A half-inch of mull covers the surface. The A-horizon is generally 4 inches thick and

composed of dark gray loam with little or no sand. The B-horizon extends from a depth of approximately 4 to 20 inches and is usually light gray in color. There is little silt and a great deal of clay. Some oxidation but very little leaching has taken place.

The substratum of Area III is composed mainly of coarse unstable shale fragments, although there are islands of soil in the slump area. In Area IV, the substratum is made up largely of stable shale fragments, with soil islands again present in the slump portion. Weathering has proceeded at varying rates in different localities—some being characterized by fine, well-disintegrated shale particles, whereas others still have coarse fragments. The depth of weathering also varies from less than an inch to 5 or 6 inches.

The tongues of debris in Area V are made up of fairly well disintegrated shale fragments. The soil on the intervening areas still bearing vegetation is somewhat similar to that of Area II. There is less humus, however, and even less color change between the A and B horizons. The substratum of Area VI was not carefully analyzed; it appears to be a floodplain veneered with shale fragments.

The shaly parent material was not chemically analyzed. It is known, however, that the Pierre shale contains a high percentage of calcium, and it is assumed that nitrogen content is deficient. As to the physical properties of the shale, its weak, laminated condition is conducive to rapid weathering. Contraction and expansion by the effects of alternate heating and cooling, freezing and thawing, wetting and drying are probably extremely important in the breakdown of the particles.

Biotic conditions

Effects of grazing in the area of the earthflow are noteworthy. Grazing of cattle has been restricted since the establishment of the Gunnison National Forest in 1905. However, in 1946 there were still 1200 head of cattle being grazed in the Gothic area from approximately the 15th of July to the 15th of August. A 20 per cent reduction, however, has occurred since that time. The degree of grazing done annually is largely dependent upon the efficiency of the cowboys. In some years, the cows are kept from entering the earthflow. In other years, they graze the land heavily. In dry summers, the damage is particularly notable.

Marmots and gophers, which occur abundantly on the flow, provide the only other known mammal influence. Through their activities, they probably aid slightly in the breakdown of shale particles and in dissemination of seeds.

The Vegetation

Initial stages of succession may be observed over the relatively large area bared by the earthflow, whereas late stages are represented by areas still bearing the vegetation existing previous to the flow. The approximate rate of succession may be determined because the age of the earthflow is known. Both xerarch and hydrarch successions occur; only the xerarch will be discussed, how-

Fig. 4. Map of the distribution of the plant communities on the Gothic Earthflow.

ever, because hydric conditions occur only locally along seepage areas and surrounding the meanders of East River near the lower margin of the earthflow.

In order to record the entire vegetational cover of the earthflow as it appeared in 1947, the distribution of distinctive mosaic patterns of species populations was mapped by plane table and alidade (Fig. 4). Line transects and list quadrats were employed to determine the variation in composition within these communities. Three transects extended the length of the flow, and another was laid parallel with one made by students from Rocky Mountain Biological Laboratory in 1940. At least two 10 x 10 m. list quadrats were located in each area. In addition, twenty 1 x 1 m. quadrats were made in Area II and in the remnants of original vegetation of Area V. All of these quadrats were located at random. Ten permanent quadrats also were located in 1947. They were carefully placed with reference to survey stations; wooden stakes, cairns, and reference stones mark the corners. These permanent quadrats have been charted every year since 1947, with the exception of 1953, and in some cases photographed.

The majority of the species populations were determined through use of the current manuals for Colorado (Weber 1953, Harrington 1954). However, I wish to acknowledge the assistance of the following people for either determining or verifying specimens in their special groups: Lincoln Constance, Umbelliferae; G. J. Goodman, *Eriogonum;* H. D. Harrington, Compositae and Gramineae; D. D. Keck, *Penstemon;* E. T. Wherry, Polemoniaceae. In addition W. A. Weber, University of Colorado, checked the collection as a whole. A reference collection of species, serving as vouchers for the names used in the paper, is deposited in the herbarium of the University of California at Berkeley.

Description of the communities

The xeric communities

The communities (mosaic patterns of species populations) on the earthflow appear to be correlated with the relative stability of the substratum and the degree of soil development. Areas I, III, and the steep portions of Area V provide uncertain anchorage for plants; however, Area I is composed of soil whereas Areas III and V are made up of shale fragments. Areas IV, VI and the gentle flow portions of Area V provide a stable substratum composed of shale fragments. A well-developed soil profile characterizes Area II and the remnants untouched by flow debris in Area V. On the unstable areas, the population patterns consist of almost pure stands of either *Chaenactis alpina, Rosa woodsii,* or *Senecio atratus.* The stable shale areas are occupied by a mixture of perennial forbs; the fescue and sagebrush communities occur on well-developed soil.

The Chaenactis alpina community.—Chaenactis alpina occurs in relatively pure stands on a substratum of loose, unstable shale fragments. It also occurs, with varying density, over the flow areas which have a stable substratum. Complete dominace by the species, however, is the diagnostic criterion of the *Chaenactis alpina community.*

Indicative of the variability in this species population is the considerable disagreement concerning its nomenclature. Stockwell (1940) reports that individuals included within this species generally exhibit wide geographic variability in morphological characters. In the eastern portion of its range (which includes western Colorado), segregates of *Chaenactis alpina* form isolated colonies of relatively uniform populations, although differentiation as yet had not progressed to the point where these colonies merit separate taxonomic status.

The most common habitat of *Chaenactis alpina* in the Gothic area, as well as in the Elk Mountains in general, is on shale slides at elevations from 8,000 to 10,000 feet. From 10,000 to 13,500 feet, it is characteristic of siltstone and sandstone talus slopes, but it has been observed only rarely on limestone and igneous rocks. It is also present along trails, abandoned roads, and other scars, here also most common on shale or soils developed from shaly parent materials.

The individuals observed in the Gothic area are perennials which vary in height from about 5 to 20 cms. The root systems of those plants growing on stable shale differ considerably from those growing on unstable shale. In Area III, *C. alpina* is one of the few species able to maintain itself. Excavations were made here of several average-sized plants. Large, woody taproots which give rise to an extensive secondary system were revealed. In some cases, adventitious roots developed where the stem had become buried. The continued development of these adventitious roots as burial of the stem progresses, is, of course, a great advantage to a plant growing on such a highly unstable substratum. In addition to adventitious roots, there are usually 2 to 5 rootstocks, each of which is terminated by a caespitose leaf cluster. Excavation of root systems of several plants on stable conditions of Area V showed that here the taproot is neither large nor particularly tough. The secondary system is extensive, but the branching is more compact than on those plants

from Area III. No adventitious roots were found on plants growing under stable conditions. However, rhizomatous proliferation of the plant was as common on stable as on unstable substratum. This may be important to the persistence of the species population, for it enables reproduction when conditions are unfavorable for germination of seeds. Also the root systems in both stable and unstable shale were sufficiently deep to utilize moisture at a depth of 12 inches or more. Since adequate soil moisture may be a limiting condition, a deep root system may be selective for *C. alpina*. The achene has a prominent scaly pappus that forms a crude parachute; thus wind is probably the most effective agent of dispersal, with birds and mammals less likely. Abundant germination of seedlings has been observed throughout the summer, but the greatest number seems to appear in August.

The date of establishment of *C. alpina* after the occurrence of the earthflow is unknown. Although no data are currently available concerning the physiological capacity of the individuals of this species population, evidence from observation indicates that they thrive under extreme conditions of instability, insolation, and consequently high temperatures and low moisture near the surface of the substratum. They thus appear admirably fitted for the pioneer role upon the bare areas produced by the earthflow, and establishment should have occurred fairly rapidly if seeds were locally available.

On the extremely unstable flow portions of Area III, *Chaenactis alpina* is the only species population which is relatively abundant, although here its density of 799/ 100 sq. m. is far less than on other areas of the earthflow. *Galium boreale* also appears on the lower portion of the slope where the shale fragments are smaller than usual. Other species which occur occasionally are *Thalictrum fendleri, Agropyron trachycaulum, Bromus polyanthus, Hydrophyllum fendleri,* and *Hackelia floribunda*. Apparently their presence in this area is due to clods of soil with enclosed plants having broken off from the vegetation on the slump block of Area II and having been carried down to Area III. Without the protecting soil clod, the roots of these plants would not be able to withstand the constant disturbance from the moving debris. As a consequence, the density of these plants is very low and there is no evidence of reproduction.

Chaenactis alpina occurs in greatest abundance on the tongues of debris in Area V. Here it reaches a density of 1042/ 100 sq. m. Although 17 other species are recorded, their total density does not exceed that of *C. alpina* alone. Important among these other species are *Eriogonum coloradense,* with a density of 167/ 100 sq. m., *Sitanion hystrix* (165), *Hackelia floribunda* (45), *Descurainia richardsonii* (37), and *Chrysopsis villosa* (27), all of which attain their greatest density in this area. Although *Artemisia dracunculus* and *Taraxacum officinale* have high density values (168, 201, respectively) they reach their maxima in other areas.

The Rosa woodsii community.—Rosa woodsii occurs in thickets on both unstable and stable shale on the earthflow; in fact on the flow it is confined to such conditions. However, in some portions of the Gothic area, *R. woodsii* occurs on well-developed soil within the fescue and sagebrush communities, not usually as thickets but as scattered bushes commonly in association with other shrubs such as *Symphoricarpos* spp., *Amelanchier pumila, Ribes cereum,* and *Prunus virginiana*. Its presence on the earthflow may be a result of the persistence of rhizomes from plants which occurred in the vegetation originally covering the area. In any event, the plants on the flow have spread rapidly to form dense thickets. Only occasionally are other plants found within these thickets, probably because the shrubby habit and dense growth of *Rosa woodsii* shade out the understory plants and monopolize the water supply.

The Senecio atratus community.—Senecio atratus occurs only on the west-facing escarpment of Area I. It grows among the boulders which have fallen from the glacial debris escarpment, the actual substratum being a talus accumulation having the character of sandy loam. Although *S. atratus* is the diagnostic species population of this community, other species populations characteristically occur along with it. *Epilobium angustifolium* is especially notable. Perennial grasses such as *Koeleria cristata, Poa pratensis, Sitanion hystrix, Stipa columbiana,* and *Bromus inermis* are invading from the slump block below, but as yet have not formed a dense population. *Rosa woodsii* occurs along the slope, but *Chaenactis alpina* is conspicuously absent. The strict segregation of *S. atratus* and *C. alpina* presents an interesting problem. The obvious factor differentiating the habitats of the two species is the nature of the substratum. *Senecio atratus* grows on the sandy loam soil of the talus where it provides stability and a fairly high water content; it probably would not survive on the loose shale where *C. alpina* grows. The root systems of the two species differ considerably. *Senecio atratus* does not have a large taproot with a widespread secondary system; neither are there adventitious roots. The roots are generally shorter, more abundantly and more compactly branched. The question as to why

S. atratus dominates on this talus, almost to the exclusion of other species populations which would seem suited to these conditions, must be left unsolved.

The perennial forb community.—The diagnostic criterion of this community is the dominance of several species of perennial forbs, although the presence of *Chaenactis alpina* is also characteristic. There are two environmental aspects of this community, one occurring in regions of slump islands in Area III and IV, and the other in the flow portions of Areas IV and V. In the latter, all former vegetation was annihilated, leaving a completely bare surface of coarse shale fragments. In the slump area, pieces of grassland are interspersed among the flow material. These not only provide local areas with a soil, but serve as a source of disseminules.

Chaenactis alpina, although still an important element, is no longer dominant as it is on the unstable shale slopes. In the flow portion its density is reduced to 557; in the slump area it is only 82. That perennial grasses and forbs are more easily established in the slump area than in the flow area is evident by the greater number of species and their greater density in the slump area. Here 58 species were recorded, whereas there are only 36 on the flow. Some forbs characteristic of both areas and with essentially the same density are: *Achillea lanulosa* (116, 107), *Artemisia dracunculus* (144, 149), *Bromus inermis* (14, 17), *B. polyanthus* (12, 15). Species with higher densities on the flow portion, however, are *Taraxacum officinale* (301, 675), and *Sitanion hystrix* (32, 135). On the other hand, species showing a markedly greater density in the slump area are *Agropyron trachycaulum* (121, 41), *Gilia aggregata* (96, 30), *Potentilla pulcherrima* (75, 2), *Penstemon strictus* (59, 24), *Erigeron speciosus* (42, 3), *Lathyrus leucanthus* (32, 16), and *Vicia americana* (15, 7). Species which occur only on the slump area, with relatively high densities, are *Vigueria multiflora* (51), *Festuca thurberi* (44), and *Stipa columbiana* (20).

The perennial forb-willow community.—Perennial forbs accompany scattered willows (*Salix barclayi* and *S. pseudolapponum*) over a large area of the floodplain, although they do not extend beyond the limits of the shale debris. Many of the species which are characteristic of the more xeric Area IV—*Artemisia dracunculus, Taraxacum officinale,* and *Gilia aggregata*—are also important on the floodplain. Other conspicuous species here such as *Melica spectabilis, Koeleria cristata, Hydrophyllum fendleri,* and *Geranium richardsonii,* however, are not common in Area IV.

The Artemisia tridentata community.—The dominance of the *Artemisia tridentata* species complex is the diagnostic criterion of this community. Although the sagebrush community occurs from approximately 8,500 to 10,000 feet in elevation within the Gothic area, it dominates only the 8,500-9,500 foot range. Here, *A. tridentata* individuals are small (15 to 24 inches in height), deep-rooted shrubs. It should be emphasized, as Clausen, Keck, and Hiesey (1940) point out, that the taxon referred to by the specific epithet, *Artemisia tridentata,* includes an assemblage of heteroploids adapted to different combinations of arid environmental conditions. Recent cyto-taxonomic studies (Ward 1954) indicate that there are at least diploid high altitude races, as well as both diploid and tetraploid low altitude races in the Rocky Mountains and Great Basin. Some of these races also are confined to particular edaphic conditions. In addition, hybridization of *A. tridentata* with *A. cana* and *A. spiciformis* of nearby areas further complicates the systematics. At the present time, the individuals in this area can only be considered part of the *Artemisia tridentata* complex, although in all probability they represent a race that is physiologically distinct from others in western North America.

The totality of dominance of *A. tridentata* is not adequately depicted by the recorded density of 175/ 100 sq. m. because of the large size of the individuals. Characteristic species accompanying *A. tridentata,* with their frequencies and densities, are: *Taraxacum officinale* (60%—630), *Artemisia dracunculus* (55%—25), *Potentilla pulcherrima* (45%—91), *Hackelia floribunda* (40%—120), *Lathyrus leucanthus* (35%—65), *Vicia americana* (30%—120), *Lupinus sericeus* (30%—33), and *Chrysothamnus viscidiflorus* and *C. parryi* (30%—33). *Chaenactis alpina* also occurs occasionally on the undisturbed remnants of Area V, having strayed from the tongues of debris onto areas which have a veneer of shale masking the underlying soil.

The Festuca thurberi community.—The diagnostic criterion of this community is the dominance of *Festuca thurberi,* although numerous associated grasses and forbs are characteristic. This grassland pattern occurs from 8,500 to 12,500 feet in the Gothic area, being most extensive from approximately 9,500 to 10,500 feet. It occurs predominantly on south exposures and on deep soils. *Festuca thurberi* is a perennial bunch grass which is one to two feet high in early summer and tends to give a knobby appearance to the grassland. In

the late summer, however, when the grass is fruiting, it forms a tall, dense stand. Its root system is extensive but shallowly placed, and the bunches enlarge rapidly by tillering. As with *Artemisia tridentata,* the dominance of this species is not adequately depicted by the density value of 489/100 sq. m. because of the relatively large size of the individual clumps. The most prevalent species occurring with *Festuca thurberi* are also the most conspicuous in both the perennial forb and sagebrush communities. They are, with frequency and density: *Achillea lanulosa* (85%—565), *Taraxacum officinale* (85%—350), and *Artemisia dracunculus* (70%—425). Several forbs exhibit the tendency to form societies with low frequency values and relatively high density. These are *Erigeron speciosus* (45%—156), *Penstemon strictus* (45%—110), *Gilia aggregata* (40%—156), and *Epilobium paniculatum* (30%—145). A number of grasses also occur, but their frequency and except in one case, their density values are relatively low. They are *Sitanion hystrix* (40%—56), *Koeleria cristata* (30%—70), *Bromus polyanthus* (30%—40), *Stipa columbiana* (30%—35), *Agropyron trachycaulum* (25%—389), and *Poa pratensis* (15%—35).

The Hydric Communities

Hydric communities occupy much of Area VI and the seepage zones in Areas IV and V. Although these communities are of little importance when compared with the xeric ones, they deserve mention.

A zontation of three communities commonly occurs in areas with permanent surface water. *Carex aquatilis* and *C. rostrata* occupy the center. The next zone outward develops a sedge mat and is essentially composed of several species of *Juncus* and showy hydric herbs such as *Spiranthes strictus, Pedicularis groenlandica, Iris missouriensis,* and *Gentiana thermalis.* The outermost zone is a dense growth of willows.

A *Veratrum californicum* community occurs in but one locality on the earthflow—in the basin of the former reservoir above Area I. It is composed almost entirely of *Veratrum* with a few mesic forbs such as *Mertensia ciliata, Heracleum lanatum,* and *Osmorhiza occidentalis.*

Aspen groves occupy the moist areas created by seepage bounding the earthflow, although not occurring characteristically in hydric conditions in the Gothic area. The understory in these groves is not dense; the most conspicuous species are *Ligusticum porteri, Bromus ciliatus, Aquilegia coerulea, Pseudocymopterus montanus,* and *Epilobium angustifolium.*

Successional relationships

Two sources of evidence are available from which to establish trends in the succession of species populations on the earthflow. First, as we have seen, distribution of the mosaic patterns of species populations is correlated with edaphic conditions which vary from those of recently bared shale to mature soil; it is these correlated phenomena which provide the basis for the establishment of an inferential successional scheme. Secondly, 7 years of records from the permanent quadrats give information concerning the actual change in species populations, which can be used to modify or confirm at least a part of the previously drawn inferences.

The communities, whose composition and distribution have been described, are presented in Figure 5 in what is intended to represent a logical developmental sequence. This developmental sequence is inferred from the known sequence of changes related to the stability of the substratum and all of the concomitant conditions occurring in the development of a soil profile. The recognition of patterns of species populations as representing stages in succession should not give the false impression that succession proceeds unitarily in an orderly, regular manner from one stage to another. On the contrary, it is to be emphasized that the communities consist of individuals, each with particular genetically-determined physiological capacities which permit their selection by conditions patterned in an environmental mosaic. With the change in environmental conditions, there is a consequent succession of kinds of individuals, each succeeding type with the capacity to occupy the particular changed conditions. Thus in succession we are dealing with problems of natural selection involving the establishment and continued sanction of individuals by the environ-

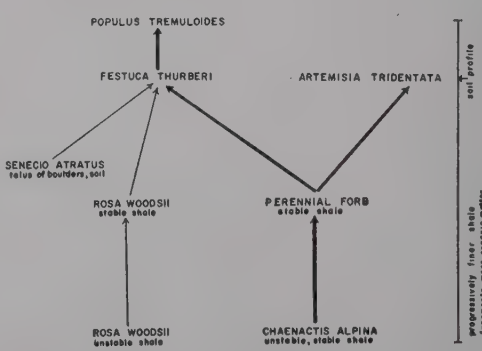

FIG. 5. Successional relationships of the xeric communities on the Gothic Earthflow with general edaphic conditions indicated.

ment. The apparent "flow" of individuals, representing different species populations, is continuous through and between what at any given point in time the observer may choose to recognize as a spatial aggregate pattern in a stage of succession.

Three distinct sequences of stages characterize the successional patterns on the earthflow. Two of them are somewhat secondary to the major sequence of succession. One, the pioneer *Senecio atratus* stage, occurs only on talus composed of a mixture of soil and rock. The most characteristic associates of *Senecio atratus* are grasses which are also characteristic of the fescue stage. Therefore it can be inferred that here succession is proceeding without intervening stages directly toward the development of the pattern of the fescue stage. This telescoping of a pioneer stage with one high in successional rank can be assumed to result from the comparative stability and advanced composition of the substratum.

Secondly, the ecological history of *Rosa woodsii* provides a puzzling problem, for it occurs not only as thickets on both stable and unstable shale, but also as scattered shrubs on well-developed soil in the fescue and sagebrush communities. It thus appears to be a ubiquitous species population capable of occupying all of these combinations of environmental conditions. For convenience, however, the dense thickets which it forms when it pioneers on bare areas are referred to here as a separate stage of succession. The thickets are self-maintaining and are exclusive of other patterns of species populations. These thickets are not formed in association with other shrubs in more populous communities. Apparently, the primary stages of soil development are favorable to extensive rhizome development. As a mature soil is formed, it seems that rhizome development is inhibited.

The third and major sequence of succession, beginning with the *Chaenactis alpina* stage, is the most complete and clearly demonstrable. *Chaenactis alpina* is definitely the pioneer species on unstable shale, and it is evident no group of plants now present will succeed it until stability of the substratum has been attained. On stable shale, however, there is some uncertainty as to whether *C. alpina* alone plays the pioneer role or whether it has been accompanied by perennial forbs on the bare, stable surface. There is no direct evidence now known to answer this question. However, comparison of line transects charted across approximately the same area in 1940 and 1946 indicates that the dominance of *C. alpina* was more pronounced in 1940 than in 1946. Also, with the progressive decrease in numbers of *C. alpina*, there has been a consequent increase in perennial forbs. In 1940, there were only 11 species and a total of 344 plants present, and *C. alpina* made up 78.6% of this total. In 1946, there were 30 species present among a total of 711 individuals and *C. alpina* had decreased to 44.3%. Thus in a period of six years, the percentage of *C. alpina* had decreased 34.3%, the number of species represented had almost trebled, and the number of individuals doubled.

Further evidence for such relationships has been obtained from the 4 permanent quadrats established in the *C. alpina* community on stable shale (3 in Area IV and 1 in Area V) in 1947 and charted each year (except 1953) through 1954 (Figs. 6, 7, 8 and 9). Marked decrease in the numbers of *C. alpina* began in 1948 in quadrats II, III, and IV, and in 1949 in quadrat I. There was a general increase in the number of *C. alpina* in all 4 quadrats in 1950, but there were less than half the number of individuals present as there were in 1947, with the exception of quadrat I. No environmental data correlative with this interesting upswing in numbers in 1950 was discovered. From 1950 to 1954 the decrease in numbers of *C. alpina* was progressive in all 4 quadrats. Comparative figures for 1947 and 1954 show the fol-

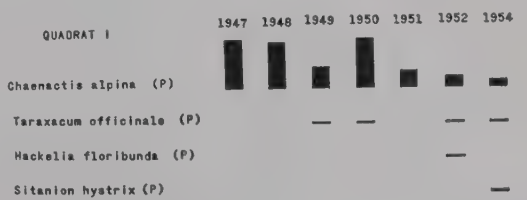

FIG. 6. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat I (*Chaenactis alpina* community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

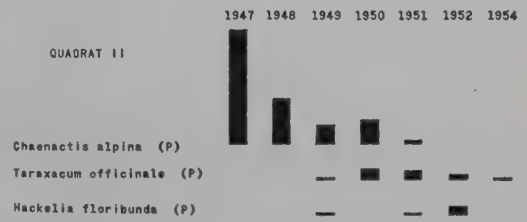

FIG. 7. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat II (*Chaenactis alpina* community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

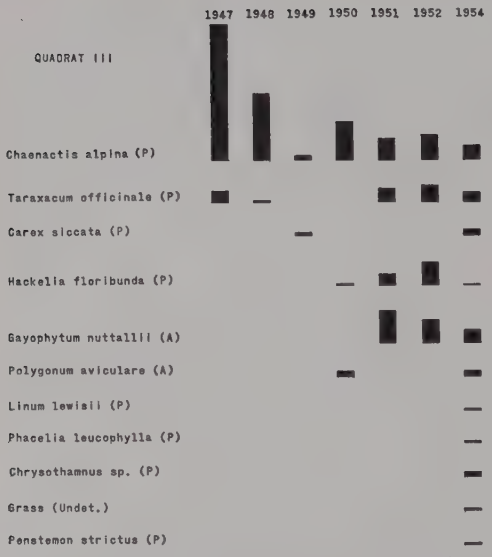

FIG. 8. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat III (*Chaenactis alpina* community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

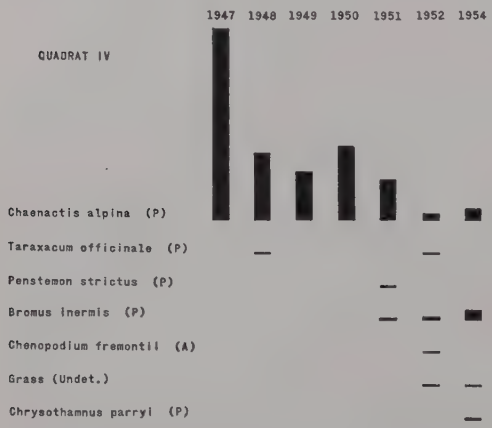

FIG. 9. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat IV (*Chaenactis alpina* community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

lowing reductions in numbers of *C. alpina* for the quadrats: I, 27—4; II, 82—9; III, 66—0; IV, 115—7. The increase of species populations of perennial forbs with the decrease of *C. alpina* was also marked. In 1947 and 1948, *C. alpina* was the only species occurring in quadrats I and III, while only *Taraxacum officinale* was present in addition in quadrats II and IV. From 1949 to 1954, 12 additional species were found on the quadrats, 11 of which were present in at least one quadrat in 1954. With the increase in the number of species, however, there has not been a resulting increase in the number of individuals per unit area. A relatively pure population of *C. alpina* appears to contain many times the individuals present in a mixed population such as the one with 13 species. However, it may be partly a matter of more surface of the substratum being covered, because each rhizome in *C. alpina* terminates at the surface in a rosette leading to a possible source of inaccuracy as regards the number of individuals involved. Despite attempts to minimize these possibilities for inaccuracy, determination of the extent of an individual from the aerial portion of the plant was never certain. Actual excavation of the plant would have been necessary.

Three of the species occurring in these quadrats were annuals and the remainder perennials. Although annuals are not abundant at the altitude of the earthflow, it seems surprising that so very few occur in the early stages of succession. Also the annual populations which do occur—*Polygonum aviculare, Chenopodium fremontii,* and *Gayophytum nuttallii*—have appeared on the quadrats only since 1950. The perennial species which occurred in 1954 are *Sitanion hystrix, Bromus inermis, Hackelia floribunda, Phacelia leucophylla, Carex siccata, Dracocephalum parviflorum, Linum lewisii,* and *Chrysothamnus parryi.* Thus, the pattern dominated by *Chaenactis alpina* in 1947 had by 1954 evolved to one dominated by species populations characteristic of the perennial forb stage. Change in edaphic conditions is a possible explanation for the increase in the number of perennial forbs and grasses. This involves the breakdown of the originally coarse fragments to a body of comparatively fine texture, together with the gradual addition of organic matter and associated increase of moisture near the surface. Moisture near the surface of the substratum may be particularly critical for germination and establishment of some of these species populations.

The perennial forb stage is recognized when such forbs as *Artemisia dracunculus, Gilia aggregata, Eriogonum coloradense, Erigeron speciosus, Penstemon strictus, Achillea lanulosa, Lathyrus leucanthus,* and *Vicia americana,* and grasses such as *Sitanion hystrix, Agropyron trachycaulum,* and *Bromus inermis* dominate the pattern of the community. This mosaic pattern of species populations is characteristic on stable shale, but where there are interspersed slump islands of soil the abundance of both perennial forbs and grasses is greater. Records from 4 permanent quadrats in

the perennial forb community (three in Area IV and one in Area V) (Figs. 10, 11, 12 and 13) show that while most of the species populations mentioned above as characteristic of the perennial forb stage have occurred in the quadrats, there are only a few which have been consistently present throughout the 7 years' period. These are *Taraxacum officinale, Artemisia dracunculus, Gilia aggregata, Sitanion hystrix,* and *Agropyron trachycaulum.* Twelve species populations were added to the 11 present in 1947, but only 8 of them were still present in 1954. The appearance, disappearance, and reappearance of certain species populations within the years observed seems to indicate the essential chance occurrence of individuals on any local site. Therefore the number of species populations, as well as their relative abundance, fluctuates yearly depending upon the vagaries of dissemination and the precise local sequence of favorable conditions probably critical at the time of germination. These fluctuations may be exceptionally great in an environment of this sort.

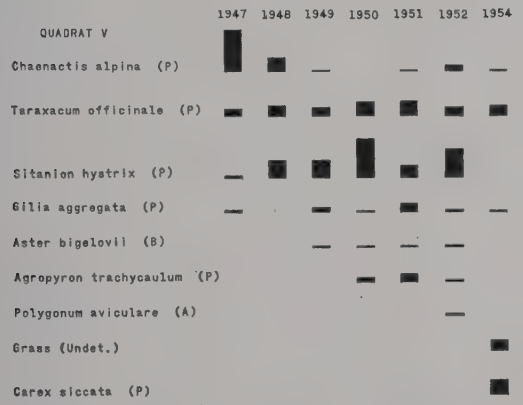

FIG. 10. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat V (Perennial forb community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

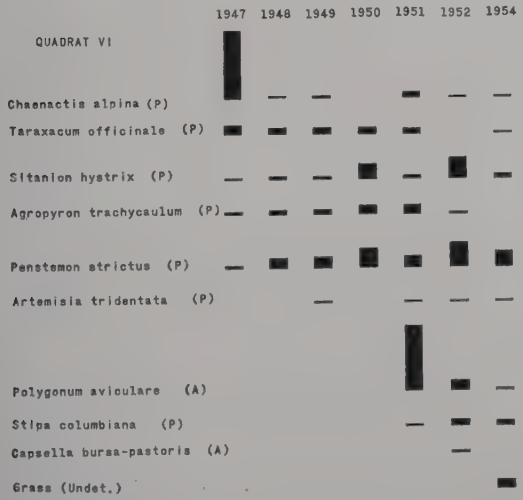

FIG. 11. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat VI (Perennial forb community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

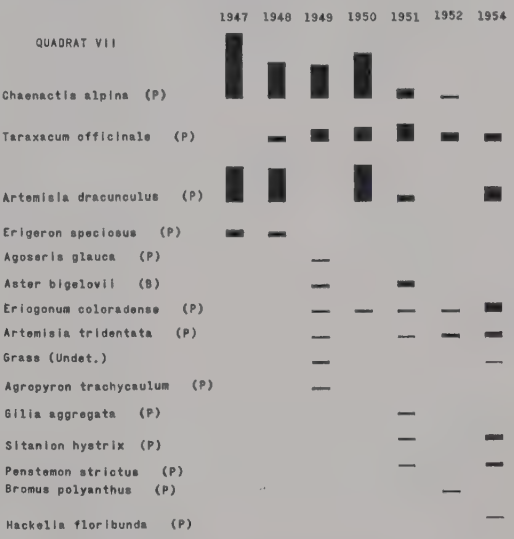

FIG. 12. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat VII (Perennial forb community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

In addition to an increase in the number of species populations, there is also an increase in the total number of individuals occurring in all of the quadrats. There were a total of 189 in 1947 as compared with 225 in 1954, although there was a wide yearly fluctuation in the total number of individuals present. In each case where a high total number of individuals occurs in a quadrat, it consists in a large part of a single species population. Such was the case in particular years with *Chaenactis alpina, Sitanion hystrix, Artemisia dracunculus, Taraxacum officinale,* and *Polygonum aviculare.* It thus appears that during certain years conditions are particularly favorable for certain species populations. This suggests that not only is the condition for establishment significant, but especially in the case of perennials the conditions for continued sanction are also involved.

Although *C. alpina* was not as abundant in the perennial forb community as in the *C. alpina* community, it was well-represented in these quadrats in 1947. By 1954, it was near extinction. The

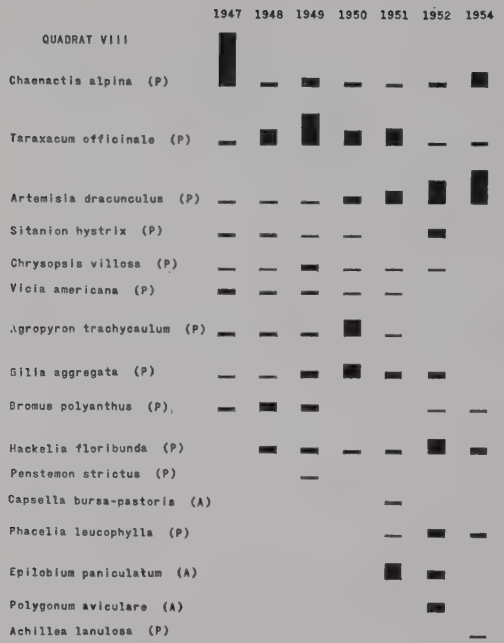

FIG. 13. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat VIII (Perennial forb community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

abrupt decrease in numbers began in 1948 in quadrats V, VI, and VIII, but did not begin until 1950 in quadrat VII. Comparative figures for 1947 and 1954 show the following reduction in *C. alpina* in the quadrats: V, 24-1; VI, 38-1; VII, 38-0; VIII, 32-8.

A decrease in numbers of a particular species population, such as that of *C. alpina,* usually has been attributed to "competition" provided by the succeeding, "successful" species populations. "Competition," however, does not furnish an explanation for the actual conditions of the environment which have inhibited the germination or establishment of *C. alpina.* Evidence indicates that for many years after the production of the bare shale area environmental conditions were such as to restrict the numbers of kinds of populations and the abundance of each. Under these conditions, *C. alpina* flourished, but it appears that the individuals in this population have a physiological capacity which allows them to occupy only the area where these restricted conditions occur within the environmental mosaic. In contrast, perennial forbs and grasses characteristic of the perennial forb stage, apparently constitute the matrix of the pattern for both of the sagebrush and fescue stages which follow. In both of these latter stages, there appears simply to be an addition of other species populations to those which define the perennial forb pattern. It thus appears to indicate that the perennial forbs and grasses have the physiological capacity to occupy a wide range of environmental conditions, as they are not only characteristic of the perennial forb stage but also of the sagebrush and fescue stages, although they occur in different densities in each. Thus, instead of being rejected completely as edaphic conditions change, only their relative abundance is affected. This variation in density provides subordinate characteristics of pattern by which to distinguish the stages, but the homogeneity resulting from the dominance of *Festuca thurberi* in one case and the dominance of *Artemisia tridentata* in the other provide the diagnostic features of the stages. The physiognomic expression of homogeneity is further aided by the abundance of several other species of grasses in the fescue community and by additional shrubs in the sagebrush community. There is no evidence now understood to explain differences in environmental conditions responsible for the development of the dominance of *Artemisia tridentata* in one case and *Festuca thurberi* in the other. They both occur on soils with a well-developed profile; analysis, however, would probably produce numerous differences in their character. For example, it might be inferred from the fact that *Festuca thurberi* has a shallow root system and therefore utilizes moisture near the surface, whereas *Artemisia tridentata* is deep-rooted and utilizes moisture at depth, that the level at which adequate water supply occurs is probably different in the two environments.

The appearance of *Artemisia tridentata* seedlings in two of the quadrats in the perennial forb community may indicate a trend toward the development of the sagebrush stage, although evidence certainly is limited. The sagebrush community dominates the 8,500 to 9,500 foot elevation zone in the Gothic area and is even more extensive in the Gunnison River Valley to elevations of approximately 7,500 feet. The community presents a relatively stable pattern here and hence is considered climax.

Records were taken from the two permanent quadrats in the fescue community in Area II (Figs. 14 and 15). As previously pointed out, the density figures for the fescue community are misleading as an indication of dominance because the amount of area occupied by an individual varies among the different species. This is particularly true regarding the bunch-forming *Festuca thurberi,* mat-forming *Eriogonum neglectum,* and

shrubby *Chrysothamnus viscidiflorus, C. parryi,* and *Lupinus sericeus.* In addition to these species, only *Artemisia dracunculus* persisted throughout the seven-year period in both quadrats. Despite the fact that the fescue community is relatively high in successional rank, there appears to be a fairly wide yearly fluctuation in the density of the subordinate species. This may be attributed in large measure to a differential in grazing as suggested by the short persistence intervals of certain of the perennial species populations. In both quadrats, there were several species populations which occurred from approximately 1949 to 1951 or 1951 to 1954. For example, in quadrat IX, *Agropyron trachycaulum* occurred from 1949 to 1951, *Epilobium paniculatum* (an annual, however) and *Koeleria cristata* occurred in 1949 and 1950, and then *Stipa columbiana, Linum lewisii* and *Agropyron saundersii* occurred from 1951 to 1954. In quadrat X, *Chrysopsis villosa, Agropyron trachycaulum,* and *Sitanion hystrix* were present from 1949 to 1952. As in the quadrats in the perennial forb community, in the years when there was a high total number of individuals this high total resulted from the exceptional abundance of a particular species population. Such was the case with *Artemisia dracunculus, Achillea lanulosa, Polygonum aviculare,* and *Taraxacum officinale.*

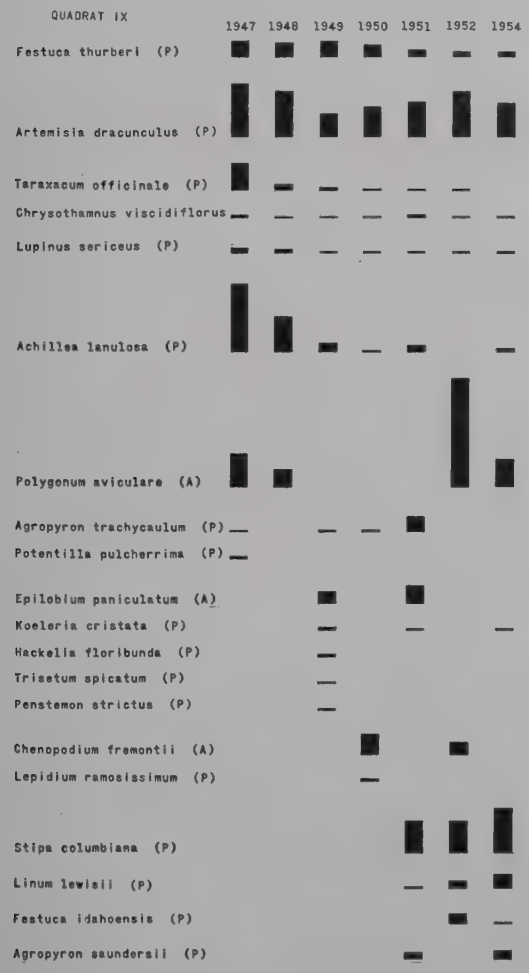

FIG. 14. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat IX (*Festuca thuberi* community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

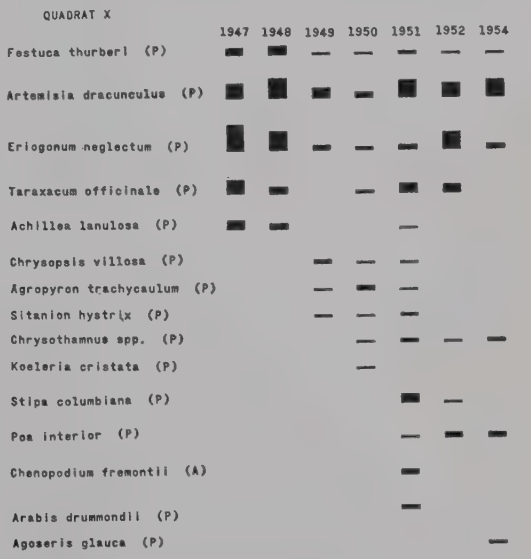

FIG. 15. Change in the number of individuals of the species populations occurring from 1947 to 1954 in quadrat X (*Festuca thurberi* community). P indicates perennial, B biennial, and A annual. 1 mm. = approximately 4 plants.

The same annuals which occurred in the perennial forb community also occurred in the fescue community. However, *Polygonum aviculare* and *Epilobium paniculatum* occurred in abundance in the fescue grassland quadrats in years previous to their appearance in the quadrats on the shale areas.

The fescue community occurs at elevations from 8,000 to 12,500 feet in the Gothic area, but is most extensive from 9,500 to 10,500 feet. Thus it occurs most commonly about 1,000 feet higher than the sagebrush community. Barclay (1941) considers this community to be an edaphic climax. She suggests that stability is indicated by the complete dominance of *Festuca thurberi* and the fact that it is self-perpetuating. She further indi-

cates that it represents the end product of definite lines of succession, because there is no evidence of invasion by any other community. Also this invasion is probably prevented by the edaphic conditions. There is some question, however, as to whether this stage should be considered climax for this area. First, the relatively pure stands of *Festuca thurberi* in some areas appear to be a result of greater resistance to grazing than are other grasses. *Festuca thurberi* is less palatable than wheatgrasses or brome grasses and therefore tends to be less molested by cattle. It also has a greater survival capacity because it proliferates by tillering as well as by seed. The relatively pure stands of fescue perhaps represent a more xeric facies than those in protected areas. In more mesic areas, fescue still domiantes, but a subordinate group of forbs and grasses is prominent. Secondly, there are indications at least in the lower altitudinal ranges of the Gothic area that the fescue community is not in all cases the end product or last stage of succession. Here the invasion by *Populus tremuloides* by means of root suckers cannot be overlooked. Once a seedling of aspen is established, the population is not dependent for further expansion upon germination and seedling selection. This situation clearly exemplifies how successional and climax conditions may be altered through natural selection by virtue of the capacities of adult members of the species populations to invade and dominate an area without involving the processes of seedling selection. This activity is at a level involving physiological processes which we usually regard as operating under environmental sanction rather than original selection. It is doubtful whether seedlings under the usual conditions could successfully invade the environment of the fescue community. But once the condition prevails and establishment occurs, asexual expansion is inevitable. Thus in the area of the earthflow where aspen is contiguous with the fescue community succession may proceed directly from the fescue stage to one dominated by *Populus tremuloides*. This then leads to the question as to whether the aspen stage is relatively stable. The aspen community in the Gothic area ranges from approximately 8,500 to 11,200 feet in elevation but it is most extensively developed between 9,500 and 10,500 feet, as is true with the fescue community. It occurs as scattered groves in the fescue community, but generally forms a continuous belt below the Engelmann spruce-subalpine fir zone. Except in areas where it has replaced burned forest, there is little evidence of *Populus tremuloides* being replaced by spruce or fir, as is generally considered the case. Therefore the pattern presented by the dominance of *Populus tremuloides* seems relatively stable under present environmental conditions and thus is considered climax at the upper altitudinal levels near the earthflow.

Summary

The Gothic Earthflow occurred probably in 1923 in East River Valley in the Elk Mountains of Colorado. It is approximately one mile long and one-quarter mile wide. The upper portion consists of a slump block with vegetation essentially unaltered by movement. The lower and major portion consists mainly of shale fragments which flowed as a result of saturation of the substratum by water acting in combination with topographic, stratigraphic, and structural conditions particularly favorable for movement. It apparently occurred suddenly and photographic evidence indicates that the present surface features and the area they now occupy seem to have resulted essentially from this initial movement. The date of occurrence was corroborated by evidence from local information, climatic data and tree-ring analysis.

A total of 5.52 inches of precipitation was received on the earthflow during a six weeks' period in July and August of 1946. This exceeded the amount received at the nearest weather station. Evaporation totals were inversely proportional to those of precipitation. Substrata on the earthflow vary from bare shaly parent material to a sandy-loam soil with a well-developed profile. The damaging effects of grazing of approximately 1,200 head of cattle fluctuates yearly.

The mosaic patterns of species populations were mapped by plane table and alidade. Nine xeric community patterns were recognized and described from data obtained from line transects and list quadrats. Changes in the species populations were recorded on 10 permanent quadrats from 1947 to 1954 with the exception of 1953.

A developmental sequence of species populations was inferred from the observed sequence of changes related to stability of the substratum and all of the concomitant conditions occuring in the development of a soil profile. Three successional lines were recognized—two of them interpreted as somewhat secondary to the major sequence. The pioneer *Senecio atratus* stage occurs only on stabilized talus comprised of a mixture of soil and rock, and there appears to be a telescoping of this stage with the fescue stage. *Rosa woodsii* is a ubiquitous species population which occurs as thickets on both stable and unstable shale but also as scattered shrubs on well-developed soil in both the fescue and sagebrush stages. For convenience,

the dense thickets that it forms on bare areas are referred to as separate stages in succession.

The third and major sequence, beginning with the *Chaenactis alpina* stage, is the most complete and clearly demonstrable. *Chaenactis alpina* is definitely pioneer on unstable shale and evidence from comparison of line transects and permanent quadrats indicates that its dominance on stable shale was once considerably more pronounced. With the decrease in the numbers of *C. alpina* there has been a consequent increase in the number of perennial forbs and grasses. Change in edaphic conditions is a possible explanation for this increase. The perennial forb stage is recognized when such forbs as *Artemisia dracunculus, Gilia aggregata, Eriogonum coloradense, Erigeron speciosus, Penstemon strictus, Achillea lanulosa,* and such grasses as *Sitanion hystrix, Agropyron trachycaulum* and *Bromus inermis* dominate the pattern of the community. These perennial forbs and grasses also constitute the matrix for both the sagebrush and fescue stages which follow. In both of the latter stages there appears simply to be an addition of other species populations to those which define the perennial forb pattern. Homogeneity is largely provided by the dominance of *Artemisia tridentata* in one case and *Festuca thurberi* in the other.

Although evidence is not conclusive, the appearance of *A. tridentata* in two permanent quadrats in the perennial forb community may indicate a trend toward the development of the sagebrush stage. The sagebrush stage in this area seems to represent a relatively stable pattern of species populations and hence is considered climax. There is some question, however, as to whether the fescue stage is climax at these altitudinal ranges. Where the *Populus tremuloides* community is contiguous with the fescue community, there is clear evidence of the expansion of *P. tremuloides* by root suckers. Thus, the stability of the grassland pattern is upset by the capacities of the adult members of *P. tremuloides* to invade and dominate an area without involving the process of seedling selection. Under present environmental conditions near the earthflow, the aspen community is interpreted as representing climax conditions because the pattern appears to be relatively stable. Thus, the line beginning with the *Chaenactis alpina* stage may terminate either in the aspen or the sagebrush stage.

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ECOLOGY OF DESERT PLANTS. IV. COMBINED FIELD AND LABORATORY WORK ON GERMINATION OF ANNUALS IN THE JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA

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In the studies of the annuals of the Joshua Tree National Monument, Death Valley, and the Coachella Valley, made prior to 1948, it appeared that the temperatures which prevailed at the time of the infrequent rainfalls were a critical factor in determining which species would germinate. The difference in summer and winter flora was shown to be due to this factor (Went 1948, 1949, Went and Westergaard 1949).

The extension of these observations in the present paper consists of the attempt to define in more detail the correlation between rainfall and temperature, and germination. The study has extended from the fall of 1948 to the fall of 1953.

It was thought that temperature, in combination with rainfall, might explain other differences than those of summer and winter, for it is a conspicuous feature of the flowering of the desert annuals that a rather small portion of the number of native species will blossom in any one year. At one time, two or three species may dominate, appearing most profusely; the following year these may scarcely appear at all, quite different species predominating. Yet three, five, or even seven years later the first ones may appear again, and in the same locations. The present study is directed toward the question whether their appearance might be due to recurrence of favorable rain-temperature

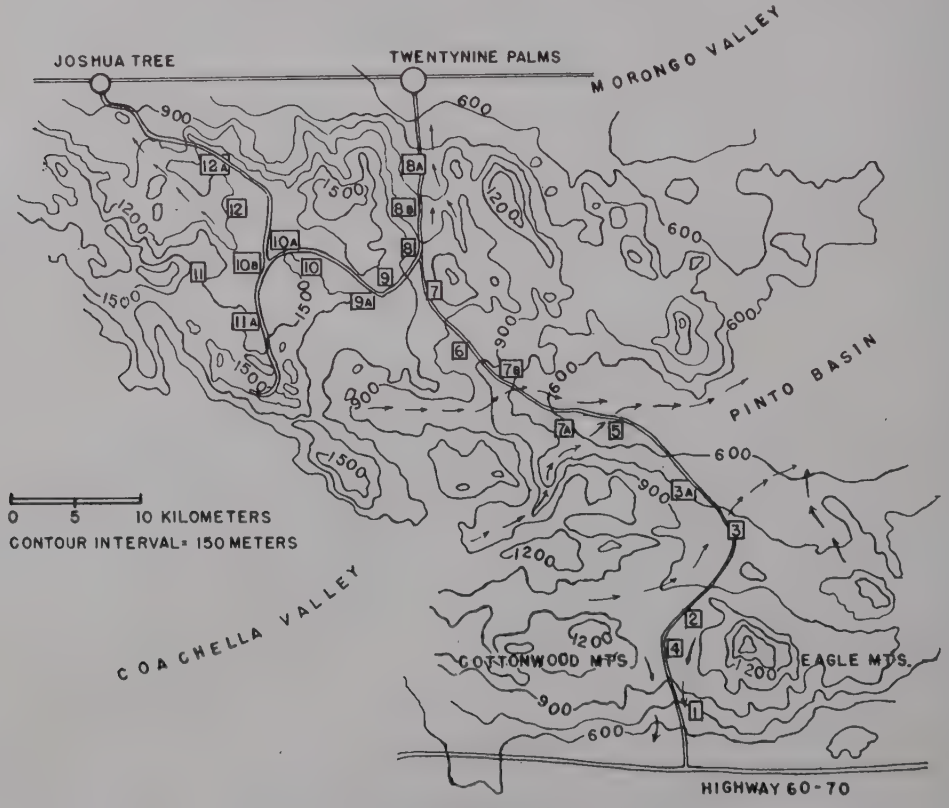

FIG. 1. Map of the Joshua Tree National Monument.

combinations. It might be that there are not in any one year enough temperature-moisture combinations during and after the few rains, to cause germination of all species if each has its own different and rather narrow requirements.

Accordingly, 17 stations were selected at approximately 3 mile intervals along the roads in the Joshua Tree National Monument. This number was later increased to 23 (Fig. 1). The altitudinal range is from 610 m. (2,000 ft.) to 1,600 m. (5,275 ft.). At each station was placed a rain gauge and a quadrat. The gauges were read after every rain by the Park Rangers.[1] Quadrats were placed on level ground, well away from shrubs.

Temperature records were furnished by the Cooperative Weather Station at Twentynine Palms. As reported previously (Went 1948), there was a mean difference of about 6° C. for an altitudinal difference of 750 meters. In tables and figures the temperatures are corrected for elevation. Preliminary experiments showed that soil temperatures were reasonably proportional to air temperatures while the soil was wet which was the only time germination was taking place.

Quadrats were visited after each rain of sufficient magnitude to cause germination, and germination counts were made. The quadrats were revisited at suitable intervals to complete identification and observe survival. When seedlings could not be identified, they were transferred to Pasadena and grown to maturity. As a preliminary study, the seedlings of the commonly occurring plants had been sketched, at the cotyledon stage and when showing the first pair of leaves. In most cases the genus can easily be recognized at this stage and very frequently the species. A few of these seedlings are shown in Fig. 2. Seedlings were transplanted from the desert with less than 1% of loss by placing them in an airtight container with a litle moist earth or paper, replanting them in sand, and watering with nutrient solution. It seemed to be more important to protect the leaves from water-loss, than to be careful of the roots, unless it was a taproot.

In 1952-53, a method of counting quadrats from stereoscopic photographs was tried. Cement bases were poured for a tripod of fixed height so that the camera could be set up in exactly the same position and height each time. All quadrats could be photographed in less than a day. This method provides a permanent record. Skill must be developed to count from photographs, and even then some species cannot be distinguished. Color might solve the problem. Herbarium specimens were taken from near the quadrat of each species found on the quadrats. These were deposited in the Pomona College Herbarium.

Soil samples were taken from the vicinity of 17 quadrats after the first rain in 1948, and were placed in various controlled conditions in the Clark or Earhart Laboratories.

[1] We gratefully acknowledge the help of Supt. S. A. King, former Supt. Frank Givens, and Supervisory Park Ranger H. L. Earenfight, whose untiring cooperation has been invaluable.

TABLE I. Germination of the more abundant annuals in the soil samples placed in various conditions of the laboratory. "Cool" = day 10°, night 3°. "Moderate" = day 17°, night 10°; day 23°, night 10°; and day 23°, night 17°. "Warm" = day 30°, night 17° and day 30°, night 23°. C = Day temp. 10°C; M = Day temp. 17°C and 23°C; W = Day temp. 30° C.

Sta.	Elev. in meters	*Eriophyllum*			*Chaenactis fremontii*			*Salvia*			*Gilia aurea*			*Euphorbia setiloba*			*Bouteloua*			*Monoptilon*			*Portulaca*			*Amaranthus*			*Pectis*		
		C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W	C	M	W
5	600	7	3	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	1	..	..	..	..	..	1	..	..	..	..	1	2
7a	670	..	1	..	..	..	..	..	..	..	..	2	..	..	..	..	..	2	3	..	..	..	..	1	..	..	..	..	..	..	..
1	670	..	..	..	..	..	..	..	1	..	2	..	..	..	..	..	..	2	2	..	..	..	..	..	..	..	..	..	..	1	..
7b	800	..	1	..	..	..	..	..	..	..	..	..	1	..	..	3	..	1	2	..	..	..	..	1	..	..	..	..	..	1	..
3	850	7	1	..	..	..	..	..	..	..	3	..	1	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	1
8a	900	2	2	..	..	..	..	..	..	..	1	..	..	..	..	..	..	2	5	..	..	..	..	..	..	..	..	..	..	..	2
4	900	..	..	..	2	..	..	3	1	..	..	..	..	..	..	..	..	..	1	9	3	..	..	..	..	..	..	..	3	1
8b	1100	..	..	..	..	..	..	..	..	..	2	1	..	..	..	2	..	..	3	..	..	..	..	..	..	..	..	..	..	3	..
6	1150	24	13	..	..	..	..	2	..	..	..	9	8	..	..	..	..	1	3	..	..	..	..	..	..	..	..	..	..	11	28
8	1200	22	13	3	..	..	..	..	..	..	2	1	1	..	..	4	..	1	5	..	..	..	..	..	..	..	..	..	..	..	..
7	1220	8	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	3	..	1	..	..	..	..	..	..	..	..	20	38
12a	1220	..	1	..	..	3	..	..	..	..	..	..	..	..	..	..	..	7	20	..	..	..	..	..	..	..	..	..	..	27	16
9	1220	..	..	..	6	1	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	1	5	..	28	52
12	1300	..	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	6	20	..	..	..	..	..	..	..	..	..	..	..	..
9a	1370	..	9	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	2	..	..	..	..	13	41	..	..	..	..	4	..
10b	1370	..	2	1	..	..	..	..	..	..	..	4	..	..	..	..	..	3	9	..	..	..	..	3	22	..	1	..	..	..	..
Totals		70	51	4	8	4	0	5	2	1	10	18	11	0	1	10	0	29	80	9	4	0	0	18	64	0	2	5	0	79	140

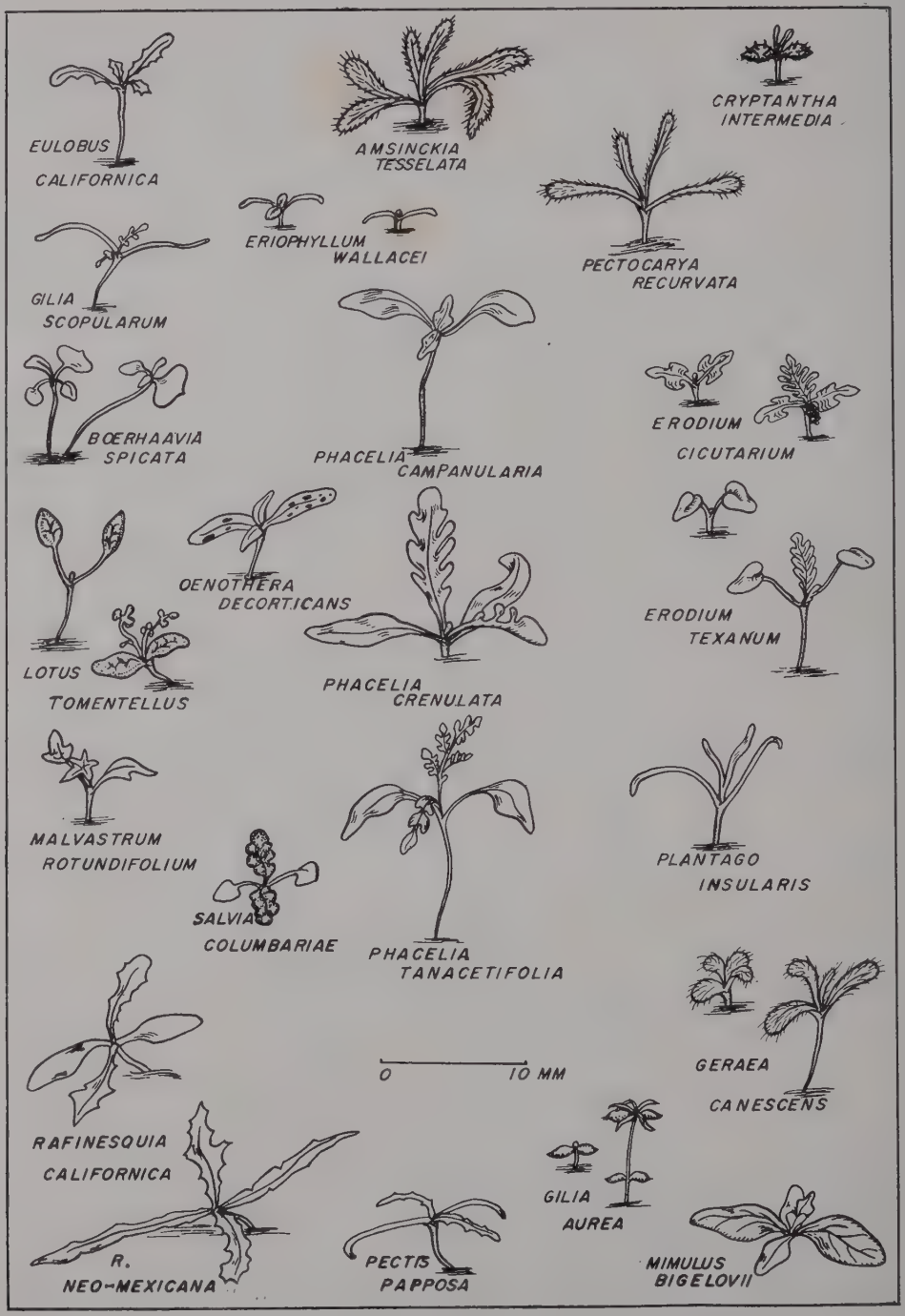

FIG. 2. Cotyledons and first leaves of some of the plants found in the Monument.

On December 30, 1948, 50 cc. of each soil sample was placed in a 4 x 18 cm. wooden flat previously filled with sand, and 100 cc. of washed sand was sprinkled over the top. Each sample was prepared in duplicate. They were then placed under a fine spray for 24 hours, outdoors. The weather was cool at this time (max. 17° C, min. 6° C) with no sun or wind. They received 550 mm. of "rain." They were then brought into the Clark temperature-controlled greenhouses and placed in 6 temperature combinations. Daily observations of the germinations were made, and each seedling marked with a colored toothpick, the color signifying the date. This simplified the daily counting of new germinations. They were sketched occasionally and identified when mature.

On July 26, 1949, after the Earhart Laboratory was in operation, either 50 or 100 cc. of soil sample (the amount depended on the estimated amount of seed in the soil from the location) was placed in a 4" x 8" plastic container previously filled with sand, and 40 cc. of sand was sprinkled over the top. All were placed in an artificial rain at a temperature of 20° C day and night. The "rain" lasted 15½ hours and amounted to 1 cm. per hour. There was a set of samples from 5 of the stations, which was not given rain; each set was kept at the same temperature and watered regularly. The containers were then placed in nine different temperature combinations (Table I) and at an 8 hr. photoperiod. The light intensity was about 400 f.c. There were two replications for each treatment for each of the samples. They were watched daily for the appearance of seedlings and a toothpick was inserted next to each new seedling.

After 11 days, when the peak of germination had been passed, some containers of seedlings in the cold conditions were moved to warm ones, and vice versa, to see if additional species would germinate. Somewhat later all were placed in daylight, in temperatures approximately the same as those in which they had germinated, so that they could flower and their identification be completed.

Results of Laboratory Work

The species whose seeds germinated in the soil samples are presented in the following lists.

I. Winter germinators (as determined by field observation).

Achyronychia cooperi T. & G.
Baeria chrysostoma F. & F. var. *gracilis* (DC) Hall
Bromus rubens L.
Chaenactis carphoclinia Gray
Chaenactis fremontii Gray
Chaenactis stevioides H. and A.
Chorizanthe brevicornu Torr.
Chorizanthe rigida Torr.
Chorizanthe thurberi Wats.
Cryptantha intermedia Gray
Cryptantha spp.
Eriogonum, small annual forms
Eriophyllum wallacei Gray
Erodium cicutarium L'Her. (introduced)
Eschscholtzia glyptosperma Greene
Eschscholtzia minutiflora Wats., var. *darwiniensis* Jones
Eulobus californicus Nutt. (*Oe. leptocarpa* Greene)
Euphorbia micromera Boiss.
Euphorbia setiloba Engelm.
Festuca octoflora Walt.
Filago californica Nutt.
Gilia scopulorum M. E. Jones
Gilia aurea Nutt.
Gilia eremica (Jeps.) Craig
Gilia matthewsii Gray
Gilia spp.
Glyptopleura setulosa Gray
Lepidium lasiocarpum Nutt.
Lepidium nitidum Nutt.
Lepidium other unidentified species, probably *L. fremontii* Wats.
Monoptilon bellioides (Gray) Hall
Oenothera decorticans (H. & A.) Greene
Oenothera spp., probably *californica, deltoides, brevipes, clavaeformis*
Pectocarya spp., probably *recurvata* Johnston; *penicillata,* (H. & A.) A. DC and/or *setosa* Gray
Phacelia crenulata Torr.
Phacelia tanacetifolia Benth.
Phacelia campanularia Gray
Plantago insularis Eastw.
Poa annua L.
Salvia columbariae Benth.

II. Summer annuals

Amaranthus fimbriatus (Torr.) Benth.
Bouteloua aristidoides (H.B.K.) Griseb.
Bouteloua barbata Lag.
Boerhaavia spictata Choisy var. *torreyana* Wats.
Boerhaavia intermedia Jones
Pectis papposa Gray
Portulaca oleracea L (introduced).
Euphorbia micromera Boiss.
Euphorbia setiloba Engelm.

After this, the plants will be referred to by the genus name alone, when only one species has been listed.

Of those soil samples which were given rain and placed in different temperatures in the Clark greenhouse, a comparison was made between the number which germinated per square meter of

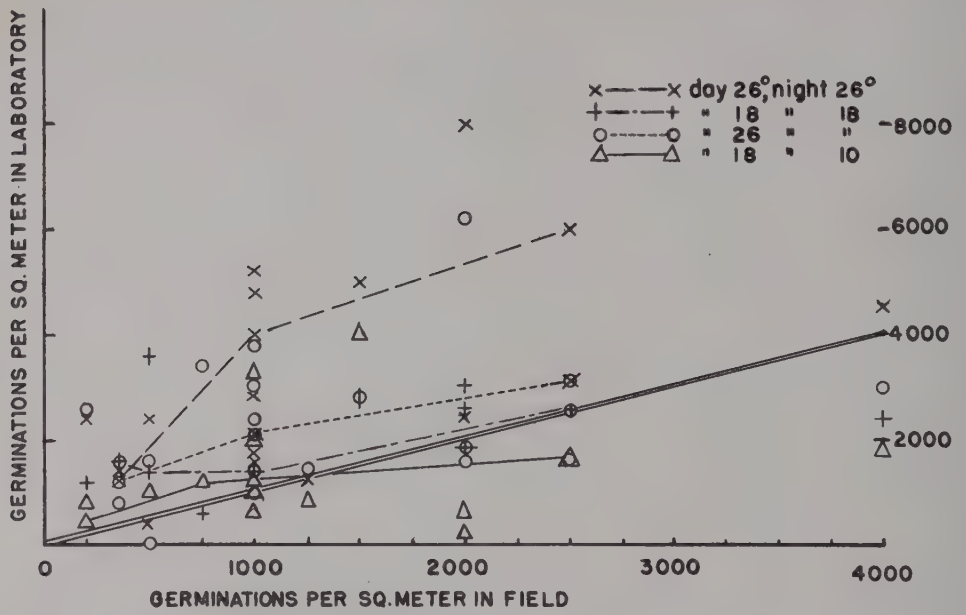

FIG. 3. Comparison of germination per square meter in the field and in the laboratory. The double line represents the ideal curve that would be obtained if there were 1 germination per sq. m. in the laboratory for every 1 in the field, in the season of 1948-49. The curves obtained for the cold temperature in which the winter annuals appeared, approximate the ideal curve fairly well. Curves obtained in the warm conditions, in which the summer annuals appeared, diverge greatly because there was little germination in the field that summer, due to lack of rain.

desert soil in the greenhouse and the number which germinated in the field in 1948-49.

At the lower temperatures (day 18°, night 10° and day 18°, night 18°), the ratio is close. At the higher temperatures (day 26°, night 18° and day 26°, night 26°) there was a large germination in the greenhouse but none in the field, because of the absence of summer rain. (See Figure 3.)

It should be borne in mind that these soil samples were taken after a rain. This rain of October, 1948, was followed by large germination in the field. Nevertheless, much viable seed must have remained ungerminated in the soil, since large numbers of seedlings appeared when the soil samples were placed in various temperatures in the laboratory.

Table I presents a condensation of the laboratory soil sample germination results. The division into cold, medium, and warm is made according to the phototemperatures, which seemed to be critical for some of the species. Nothing but winter annuals germinated in the cool temperatures; both summer and witner ones germinated in the medium temperatures. Summer annuals germinated predominantly in the warm temperatures. Of winter annuals, only a few *Eriophyllum,* never more than one to a sample, germinated in warm conditions.

Where many seedlings were expected, only 50 cc. of soil was used in the germination tests. By doubling the figures obtained, the estimated number of viable seeds per 100 cc. was obtained. All other soil samples consisted of 100 cc.

In the samples which were given no initial rain but which were watered thereafter, from one-fourth to three-fourths as many seedlings appeared in the medium temperature conditions as in control samples, in the same conditions but with the initial rain. Whereas *Pectis, Portulaca,* and *Gilia aurea* were plentiful in the controls, they did not appear in the sample which received no rain. There was a single exception to this; in the sample from Station 5, which is the lowest and hottest of all and consisted of almost pure sand, there were an equal number of germinations with and without rain, and *Eriophyllum* and *Gilia aurea* were among them.

In the warm conditions, germination in the samples without rain was in no case greater than half of the germination with rain. In one sample, there was no germination, while its control had 32 germinations. Few of the seedlings which ger-

minated survived, even from Station 5. Species which appeared plentiful in the duplicate samples were, again, *Pectis, Gilia aurea,* and *Portulaca;* of these only *Gilia aurea* appeared in the sample without rain. This confirms the field observations on the need of *Pectis* for a rainfall of at least 20 mm. (Went 1948). After light summer rains in 1953, a few *Pectis* seeds germinated after 15 mm. precipitation, but not after 10 mm. or less.

In growing the annual seedlings to maturity, it was found that given sufficient light intensity and proper photoperiod in the case of long-day plants, temperatures best for germination are also best for survival and flowering. This is what we should expect if the faculty of germination only within certain temperature limits has survival value. In the case of some species (*Pectis* and *Eriophyllum*), a change of temperature (to low or high) shortly after germination is followed by dwarfing and early flowering both in the laboratory and in the field.

In 1951, for example, there were 2 rains with the same temperatures prevailing, one in July and one at the end of August. Some *Pectis* germinated after both rains. After the July rain temperatures remained high and the seedlings developed into large plants. After the August rain, the temperature dropped and the plants were dwarfs. In the laboratory, both *Pectis* and *Eriophyllum* were dwarfed if transferred to lower temperatures.

In the Earhart Laboratory experiments, when containers were first placed in low temperatures and then placed in higher temperatures after germination semed to have ceased, *Bouteloua* (a summer annual), germinated. There was also some further germination of *Portulaca,* an introduced summer annual. When those placed first in high temperatures were changed to lower ones, *Gilia aurea* and *Eriophyllum* (winter annuals) appeared.

Not only germination, but also survival was observed both in the field and in the laboratory. As Figure 4 shows, the winter annuals not only germinated, but also survived better at the lower

TABLE II. Germination, temperature, and rainfall at Station 8, a station typical of medium elevation (1189 m.) toward the center of the Monument

Date	mm. rain	Temp. °C. day	Temp. °C. night	Species which germinated
Oct. 17, 1948	43.5	21°	9°	*Eriogonum, Erodium, Filago, Gilia matthewsii, Mentzelia* sp., *Oenothera clavaeformis, Pectocarya* sp., *Salvia*
May 31, 1949	12.0	19°	4°	1 *Bromus,* 106 *Calyptridium,* 48 *Chaenactis carphoclinia,* 50 *Cryptantha,* 250 *Eriophyllum,* 1 *Malacothrix,* 35 *Nama,* 106 *Bromus,* 1 *Anisocoma,* 400 *Erodium,* 13 *Eriogonum,* 10 *Gilia aurea,* 10 *Lupinus,* 42 *Salvia*
Nov. 10, 1949	6.2	14°	8°	No germination
Dec. 8, 1949	10.9	10°	4°	4 *Lupinus,* (germ. in Feb. There had been 4 showers since Dec.)
July 7, 1950	8.3	35°	19°	No germination
Aug. 25, 1950	5.6	39°	21°	No germination
Sept. 5, 1950	43.4	31°	17°	210 *Aristida,* 1 *Bouteloua,* 10 *Eriophyllum,* 5 *Erodium,* 30 *Euphorbia setiloba,* 20 unidentified
Jan. 11, 1951	6.3	12°	−2°	No germination
Jan. 29, 1951	11.2	16°	−1°	2, unidentified, died
April 3, 1951	8.0	24°	9°	No germination
April 18, 1951	19.5	24°	10°	No germination
May 14, 1951	9.2	20°	11°	2 *Aristida,* 2 *Bromus,* 6 *Chorizanthe,* 8 *Erodium,* 3 *Gilia* sp. *Pectis* and *Salvia* near quadrat.
Aug. 28, 1951	11.3	28°	11°	No germination
Sept. 28, 1951	6.7	31°	13°	No germination
Oct. 30, 1951	10.4	22°	3°	No germination
Nov. 22, 1951	11.9	14°	0°	No germination.
Dec. 12, 1951	7.3	11°	−2°	No germination
Dec. 29, 1951	7.0	8°	−6°	1 *Delphinium,* 33 *Erodium,* 150 *Eriophyllum,* Near quadrat: *Amsinckia tesselata, Chaenactis fremontii, Monoptilon, Oenothera decorticans, Oe. clavaeformis, Salvia*
Jan. 17, 1952	41.7	14°	1°	No germination
March 8, 1952	7.7	12°	−2°	No germination
March 15, 1952	6.0	16°	0°	31 *Eriophyllum*
April 27, 1952	5.3	29°	11°	No germination
Nov. 8, 1952	6.5	19°	2°	No germination
Nov. 14, 1952	18.1	14°	1°	No germination
Dec. 17, 1952	39.6	9°	0°	40 *Chaenactis fremontii,* 17 *Coreopsis bigelovii,* 300 *Eriogonum,* 500 *Eriophyllum,* 300 *Filago,* 130 *Gilia matthewsii,* 10 *Oenothera decorticans.*
Feb. 24, 1953	9.2	16°	0°	22 *Cryptantha*
July 11, 1953	7.2	38°	22°	No germination
July 18, 1953	9.3	40°	21°	No germination
Aug. 12, 1953	11.5	33°	15°	5 *Bouteloua*

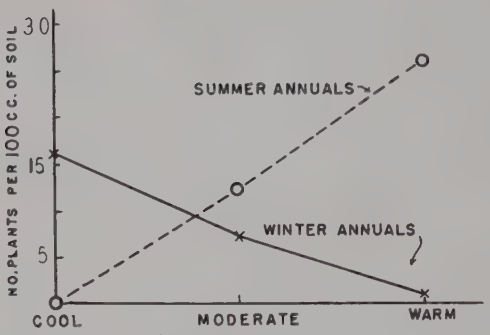

FIG. 4. Comparison of temperature optimals for summer and winter annuals when germinating in the laboratory.

temperatures, whereas the opposite was true for summer annuals. Tables IV and V give typical survival records.

RESULTS OF FIELD WORK

In reporting the field observations, it is not possible because of their extent to give the entire tabulation. Neither does it seem wise to group the stations, since the chief value is the segregation of factors. Hence it was thought best to show the full data for one station. As a typical example, the germination at Station 8 is shown in Table II. All data, however, have been considered in discussing the individual species, and are available.

Rainfall for the various stations is given in Table III. Estimated temperatures for all stations were calculated from those taken at Twentynine Palms on the basis of a decrease of 1° C for each rise of 125 meters, which seemed to be justified by previous temperature observations in various parts of the Monument.

TABLE III. Winter rainfall for various stations during each of the 5 years

Station	1948-49	1949-50	1950-51	1951-52	1952-53	Elevations
5.....	49.7	18.2	19.0	97.3	47.3	610 m.
1.....	43.5	21.8	15.1	80.4	55.2	671 m.
3a.....	—	22.1	26.2	96.4	61.9	762 m.
3.....	—	19.5	—	72.0	64.4	854 m.
8a.....	53.5	27.0	61.2	—	—	915 m.
4.....	—	27.2	19.8	—	—	915 m.
2.....	—	19.5	24.6	127.3	89.5	1067 m.
8b.....	55.8	28.0	53.3	—	—	1098 m.
6.....	53.6	31.6	33.2	123.3	72.5	1159 m.
8.....	57.7	30.8	60.4	120.5	84.7	1189 m.
7.....	55.1	36.1	—	—	73.0	1220 m.
9.....	59.8	38.3	43.6	136.6	84.8	1220 m.
12.....	80.7	58.8	60.9	158.4	—	1312 m.
11.....	57.4	53.0	78.1	143.4	94.3	1311 m.
9a.....	59.4	41.1	69.1	—	—	1372 m.
10a.....	72.8	54.5	87.1	186.6	94.9	1372 m.
10.....	50.5	58.6	85.2	165.2	92.9	1403 m.
Twenty nine Palms...	93.3	44.7	39.3	61.1	49.7	650 m.

The winter rains (September through April) have been compiled in Table III. The summer rains are even more irregular, and there were very few in the years 1949-1953. These 5 seasons have been exceptionally dry, as indicated by a comparison with the average winter rainfall of 100 mm. in Twentynine Palms, which is just outside the Joshua Tree National Monument at 700 m. elevation. In Figure 5 the winter rainfall values of 3 to 5 stations are averaged for the different altitudinal ranges. This figure shows clearly the increase in precipitation with altitude; at 1,370 m. almost twice as much rain fell as at 650 m. In the driest years, the highest stations received 2.5 and 3.8 times as much rain as the lowest, but in the wetter years, only from 1.4 to 1.9 times as much. The stations below 1,100 m. had 5.0 times as much rain in the wettest years as they had in the driest. The higher stations had only 3.3 times as much. This shows that the yearly aberrations from station to station are greater when the precipitation is less.

In general, the quadrats typified the germination of the area as a whole. This was true particularly in the years of wide-spread germination. In the more barren years, species which occasionally occurred in an area often failed to be represented in its quadrat. Their presence in the neighborhood of the quadrat was then recorded.

It may be of interest to describe briefly the general character of each of the 5 winters.

The season of 1948-1949 began with a general rain of over 40 mm. In late December, there was a heavy snowfall which covered the ground for weeks. This was not recorded by the gauges but amounted to about 50 mm. of precipitation. Therefore, moisture was probably not a limiting factor. Although nights were below freezing, plants were protected by snow. By the time the snow melted, temperatures were moderate. Rainfall for the year, exclusive of the snow, varied from 50 mm. at Station 5 to 73 mm. at Station 10a. There was a large germination. Species which were conspicuous in the blossoming period were *Gilia aurea, Gilia matthewsii,* and *Eriophyllum wallacei.* The infrequently found *Nemacladus* and *Eschscholtzia glyptosperma* were also present.

In 1949-1950, there were only two rains of any consequence, one in October and one in December. Rainfall at Station 5 totaled 18 mm.; that at station 10a, 55 mm. Average monthly temperatures range from day 16° C, night —1° in

January, to day 25°, night 7° in March. There was little germination, mostly borages and *Salvia columbariae,* with a few *Chaenactis fremontii, Achyronychia,* and *Gilia eremica.*

The winter of 1950-1951 was equally dry, and was very cold. The average minimum temperature for the first 3 weeks of January was below 0° C. Night temperatures at the higher stations were as low as —11° C. There was no snow to mitigate the effect of these temperatures. *Eriogonum, Gilia eremica,* and *Erodium cicutarium* germinated. Although at the higher stations a few seedlings were killed by frost, in the main the plants proved remarkably hardy. Many survived a period of being encased in ice, with the ground frozen.

In 1951-1952, there was a late August and a late September rain, both with temperatures of approximately day 29°, night 13°. This brought about the unusual appearance of summer and winter annuals at the same time, the former blooming while the latter were germinating. There were good rains later. Station 5 received 98 mm., Station 10a had 187 mm. There were also heavy frosts. Temperatures were moderate in the daytime (16° to 24°) and low during the night (0° to 4°). There was a very large germination and plants grew so vigorously that there was a great display of flowers. Large areas were covered with *Malacothrix californica, Eschscholtzia minutiflora* var. *darwiniensis* (very large), *Rafinesquia* (both species), *Oenothera decorticans* and *Oe. clavaeformis.* There were many patches of *Phacelia campanularia, Phacelia tanacetifolia, Monoptilon, Nama demissum, Amsinckia,* and *Draba.* For the first time since the winter of 1947, *Thelypodium cooperi, Mimulus bigelovii,* and *Glyptopleura* were noted. *Layia* and *Baileya* were more common than usual.

In 1952-1953, Station 5 received 47 mm. of rain, and Station 10a, 95 mm. There was one good general rain in February. Night temperatures were below freezing much of the time in November and December. The most abundant species were *Chaenactis carphoclinia, Erodium, Eriophyllum, Gilia matthewsii,* and *Eriogonum.*

There were good summer rains in 1951, and one in 1953. The other summers were rainless or nearly so, consequently were without germination. In 1951, all the typical summer annuals were found. In 1953, there was barely sufficient rainfall in August, at Station 8, 5, and 11 to cause the germination of the usual species. There was less *Pectis* and more annual *Boerhaavia* than usual. *Mollugo* germinated along washes but died.

Distribution of seed

As a general rule, the seed of various species are well-distributed over the area. The different stations do not have species peculiar to them; rather, the appearance of a species was correlated with the conditions accompanying a particular rain. If found germinating plentifully at any station, it was usually found at all stations where climatic conditions were similar.

An exception to this rule was Station 11b, the highest one, on a windy promontory. The stations richest in both number of specimens and of species were 10a, 10b, and 8. These were intermediate in elevetation and rainfall, located toward the center of the Monument. Stations 8a, 12a, and 1, though they contained the same species, did not show as large numbers of seedlings. These stations are around the outer slopes which rise toward the central area of the Monument. These slopes face the Coachella and Morongo Valleys, and are subjected to more wind.

Effect of heavy precipitation

The greatest total precipitation does not necessarily produce the greatest germination. In 1948-49 especially, when rainfall was very good, the best germination was correlated with the intermediate amounts of rain. This has been confirmed in the laboratory, where it was shown that the optimal artificial rain for *Baileya* is 50 mm. Soriano (1954) has shown that in the laboratory, 15-25 mm. precipitation is optimal for the germination of *Pectocarya* and certain other winter annuals.

Duration of rainfall

It has also been observed that a long rain is more effective than the same amount of precipitation in a short time. In the summer of 1951, very little germination was found following a brief torrential rain near Rancho Mirage in the Coachella Valley, while in a nearby area, there was a large germination subsequent to a slow rain of no greater total precipitation. This has been shown in laboratory experiments also (Soriano 1954). Soil samples known to contain seed of *Amaranthus retroflexus, Erodium, Malva,* etc., yielded very little germination after an artificial rain of 2 hours, whereas duplicate samples at the same temperature and receiving the same total amount of rain but over a period of 8 hours, gave excellent germination (Went, Juhren, and Juhren 1952).

Correlation of germination with season

Many species germinated when temperatures met their requirements regardless of the time of year. For example, the rain of September 5, 1950, brought forth the winter annuals *Eriophyllum, Erodium, Cryptantha, Gilia,* and *Oenothera de-*

corticans and the summer annuals, *Bouteloua* and *Aristida adscencionis*. Temperatures were 32°-17°. *Eulobus* and *Salvia* germinated in August, 1951, when the temperatures were day 28°, night 10°. *Amaranthus* was found beside the usually winter-germinating *Eschscholtzia minutiflora* and *Phacelia tanacetifolia* after the September 28 rain, at temperatures of day 28°, night 12°.

Effects of first rain on germination for the year

A great variety of species was brought forth by the first rain in October, 1948. This was a general rain which caused the Monument gauges to overflow, so was over 43 mm. There were about 10 species at most stations, with plants numbering in the hundreds and thousands. At the lower stations (day 26°, night 14°), *Phacelia campanularia* and *Dithyrea* germinated in abundance.

The first rains of the autumn of 1949 varied from 5.2 to 12.5 mm. at each station; 4 species appeared at the one station which had 12 mm. but there were only 3 or 4 plants of each. These were *Bromus, Pectocarya, Salvia,* and a *Chaenactis. Erodium,* which is not a native, germinated to the extent of 250 plants at Station 12a after 9.4 mm. of rain. Otherwise there was no germination at all. Even after the second rain there was little germination.

In the fall of 1950, there were again rains of 5.2 to 14 mm. and no germination whatsoever, even after the second rain.

The 1951-1952 season began with somewhat better rain between 8 and 15 mm., with 23 mm. at Station 5 (the sandiest and hottest), but there was no germination before the third rain, except a few *Erodium,* and an *Abronia.* Between Stations 1 and 4 there was extensive germination of *Mentzelia involucrata, Phacelia campanularia, Oenothera clavaeformis,* and other autumn-germintors. At Stations 4 and 2 a total of 20 mm. precipitation was recorded in the end of October. Later in this season there was much rain, also hoar frost (so presumably dew) and then there was very extensive germination.

Ordinarily 10 mm. of rain in the beginning of the winter season did not cause germination, but once there had been a heavy winter rain, a subsequent rain of 5 or 6 mm. would produce germination, even if the ground had dried out thoroughly in the interim. Presumably leaching of an inhibitor had occurred in the first rain; the following low temperatures had prevented the formation of new inhibitors.

Relation of individual species to rain-temperature combinations

In order to establish limits of tolerance for the various species, all the appearances of each species were listed, with the accompanying weather data. If more than 15 seedlings of the species appeared on a quadrat after a rain, conditions at the time of the rain were considered favorable. If none appeared in or near the quadrat, conditions were considered unfavorable. It was thus possible to determine limits within which a species germinates. Once a plant had appeared on a quadrat and borne seed, it was assumed that seed was present in or near the quadrat. Subsequent occasions were studied to find out whether there were rains which supplied conditions within those limits, yet were not followed by germination of the species. Both the conditions accompanying the individual rain, and those which were characteristic of the season as a whole, were considered. The results of such studies on some of the species follow. All temperatures are Centigrade.

Chaenactis fremontii appeared when day temperatures were between 12° and 30°, with night temperatures of 10° and 4°. Once only, it appeared after the night temperature had been 0°. Rainfall was always above 10 mm. unless there had been a previous rain or rains that season, when a 5.6 mm. rain was sufficient. Table I shows that in the laboratory it is a cold germinator.

Chaenactis carphoclinia was usually found when day temperatures had been between 15° and 19°, night temperatures between 1° and 4.5°. It appeared many times after the night temperatures had been below 0°. The lowest temperatures at which it germinated were 4.5° day and —3.9° night. It never germinated after a first rain of less than 10 mm., but once appeared after a 2 mm. rain preceded by snow. Intermittent germination occurred, that is, the species that appeared in November, did not appear after January rains, but germinated again after a March rain. Temperatures in November and in March were optimal for it, but in January they were lower than any which have accompanied its appearances. *C. fremontii* and *C. carphoclinia* were found only once growing simultaneously in the same quadrat; on this occasion the former appeared a month later than the latter, which was in harmony with their temperature preferences.

Calyptridium monandrum germinated when the day temperatures were between 14° and 25°, night temperatures between 1° and 9°. On 2 occasions, 1 or 2 plants appeared when the night temperature was 0°. It germinated after the first rain of the season only once, when the rain was of over 40 mm., at other times only after later rains of not less than 11 mm. It always appeared when optimal conditions were satisfied.

Eriophyllum wallacei usually occurred when day temperatures were 19° or 20°, night temperature from 3° to 8°. It germinated occasionally when day temperatures were as high as 30° or as low as 11°, with corresponding night temperatures of 2° to 16°. It was never found after a rain of less than 12 mm. unless there had been previous rains in which case 7mm. sufficed. On many occasions, these conditions were satisfied, yet *Eriophyllum* did not appear. The enormous germinations which occur at times, the many areas that are covered, and the frequency with which it comes up in soil samples, indicate that there is plenty of seed. *Eriophyllum* is at its best when there has been snow, and succeeds well in the greenhouse, where it is watered frequently. These considerations point to leaching as a critical factor. In the laboratory, it germinated predominantly in the cold conditions.

Amsinckia vernicosa appeared only when night temperatures were very low, —1° to —6°, and 7 mm. was the minimum rainfall. It was an intermittent germinator. On a few occasions, it failed to appear when temperatures were optimal for it.

Coreopsis bigelovii germinated when day temperatures were between 11° and 21°, night temperatures between 1° and 5.5°. It has come up after a first rain of 12 mm., a fourth rain of 6.6 mm. The large germinations, however, appeared after rains of 30 to 43 mm.

Plantago insularis occurred when day temperatures were between 4° and 20°, night temperatures between 0° and 9°. It did not appear when nights were below —1°.

Gilia aurea germinated when day temperatures were between 9° tnd 26°, night temperatures between 0° and 10°. Rainfall was always 10 mm. or more.

Baileya pauciradiata and *multiradiata*. No difference in climatic response was observed in these species. They both germinated when the day temperature was between 16° and 29°, night temperatures between 5° and 9°. It is possible that the day temperature could be higher. Seven mm. of rain was sufficient. In the Monument, *Baileya* has not been found below 1200 m.

Salvia columbariae was found when day temperatures were from 10° to 31°, night temperatures 0° to 11°, but most of its appearances followed day temperatures of about 18°, night temperatures of 2° to 4°. A rain of 12.5 mm. was sufficient to cause germination.

Amaranthus fimbriatus was found when day temperatures were between 28° and 35°, night temperatures between 12° and 20°. First rains of only 6 mm. were sufficient for it. It sometimes germinated for a second time in a summer, but did not do so when the second rains were heavy, of 23 to 50 mm. This seems to agree with the other evidence that large amounts of rain are deterrent to its germination.

Pectis papposa appeared after any of the summer temperatures, day temperatures of 28° through 40°, night temperatures of 13° to 21°. Only when the first rain was of as much as 12.5 mm. did *Pectis* appear; and if subsequent rains were of at least 9.5 mm. A 22 mm. rain brought forth enormous numbers of seedlings at Station 9 when a previous rain of 9.3 mm. and similar temperatures, had not been followed by germination.

Occasionally (though by no means frequently, and not in our quadrats) *Pectis* has germinated in early fall when temperatures were definitely lower than summer temperatures; in the laboratory also it has come up in soil samples placed in moderate temperatures. Both in the field and in the laboratory it is then much dwarfed. In the laboratory it germinated predominantly under warm conditions (Table I).

Boerhaavia spicata and *intermedia* appeared under widely differing conditions, rains of from 6 mm. to 51 mm., with day temperatures between 21° and 39°, night temperatures between 12° and 30°. In spite of this wide tolerance. it did not appear after every summer rain, when these conditions were offered. On 4 out of 5 appearances, it germinated after the second rain of the summer, not after the first. However, on one occasion it did germinate after the first rain, which was of only 6 mm. The scarcity of summer rains, and especially on the same quadrat, prevented the obtaining of much evidence. The species is not a prolific seeder, and it may be that this is the reason for its non-appearance under favorable germinating conditions.

Discussion

In this investigation, an attempt has been made to correlate laboratory results and field data in a dual effort to explain field observations with quantitative and controlled experiments, and to show that behavior of plants in the laboratory parallels that in the field provided laboratory conditions duplicate the significant factors controlling development of the plant in nature.

The principal factors which determine the germination of annuals in any given season in this area are the amount and duration of precipitation and the temperatures which prevail while the soil is wet. Each species has definite and rather narrow limits of tolerance and is not found in quantity except when conditions are within these limits. In consequence, much viable seed remains ungerminated in the soil from year to year, even after

heavy rains, which can be induced to germinate if placed in suitable conditions. Leaching is also an important factor. It is brought about best by slow rains, or by a heavy initial rain followed by light sprinkles at intervals, or in the case of winter germinators by snow remaining on the ground.

While species are not found germinating outside of their limits of tolerance, they are not always found when seemingly, conditions within these limits have prevailed. This failure to appear could be due to absence of seed in the particular areas, or to factors as yet unknown.

In previous work, it was shown that desert annuals can be segregated into winter and summer germinators (Went 1947, 1948). This distinction was made by Shreve (1951) for Sonoran Desert plants. It also was shown that a definite amount of precipitation was necessary before these plants germinated. Both these facts were confirmed and extended in the present investigation. From Table I and Figure 3, it is clear that desert annuals can be divided according to the temperatures at which they germinate and at which they survive. The low temperature germinators (*Eriophyllum, Chaenactis, Gilia aurea*) survived best at the lowest temperatures at which they were tested in the greenhouse (10° C day, 3° C night), and when they had germinated at all at the higher 30° C day and 17° C or 23° C night temperature, they later died. Exactly the opposite is the case for summer germinators (*Pectis, Bouteloua, Portulaca* and *Euphorbia*). In the field plots, the distinction between summer and winter germinators was more pronounced than in the laboratory, where at intermediate temperatures (day 17° C and 23° C with night at 10° C-17° C) both groups germinated in equal numbers. This was never observed in the field. Although once in autumn a few summer annuals germinated with large numbers of winter annuals, and in the late summer a few *Eriophyllum* were found in shaded spots together with much *Pectis* and *Bouteloua,* on the whole there is no doubt that the difference between summer and winter germinators is primarily a question of temperature during germination. The reason that some summer germinators appeared in cool conditions in the laboratory, may have been that during the 12-24 hour rain period all seedling flats were exposed to the same temperature (17° C-20° C). Only afterward were they brought into different temperatures. Also, neither warm nor cold temperatures are so extreme in the laboratory as in the field.

There was no yearly rhythm in germination such as Bünning has observed with several plants or Barton in *Amaranthus* (Barton 1945), for our germination tests have been carried out at different times of the year and each time the same two groups of warm and cold germinators developed.

The collected data are most interesting in connection with the rain observations. On account of the irregularity of rains in the desert, both in respect to space and time, it was necessary to have a rain gauge installed next to each ecological station. These gauges were distributed over an altitudinal range from 600-1300 m. above sea level, and as Fig. 5 indicates, the amount of precipitation is greater at higher altitudes. The Joshua Tree National Monument lies east of the San Bernardino and San Jacinto mountains, which are over 3,000 meters high, and relatively little moisture is left in the atmosphere after the moist air from the Pacific has passed over them. At 100 m. elevation west of these mountains, the average annual rainfall is 400 mm. At 100 meters in the Monument, it is likely to be only 25 mm. (See Fig. 5). The measurements were made in dry years. Precipitation at this elevation would be about 50 mm. in normal years. (In Death Valley further northeast, at sea level, annual winter precipitation amounts to 30 mm. per year.)

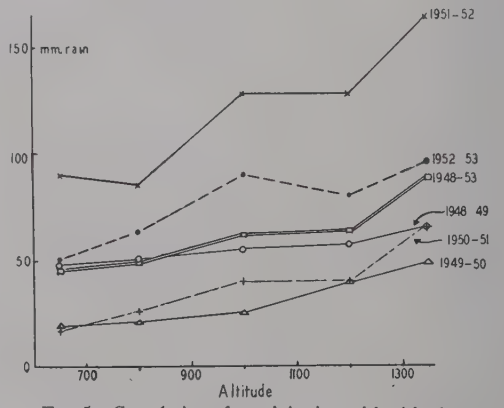

FIG. 5. Correlation of precipitation with altitude.

The years over which the project has ranged (1948-1953) were exceptionally dry, all but 1951-52. This can be seen in the field by the many dying or dead shrubs of *Larrea* (*e.g.,* near Station 4a), *Dalea spinosa* (near Station 5), *Juniperus* and especially (near Station 3) smaller plants like *Franseria dumosa* and *Hymenoclea.* Summer rains, coming as local thunderstorms, were almost completely absent, and the splendid display of *Pectis* and other summer annuals in 1945 has not been repeated. In the summer of 1953, a rain of 9-12 mm. occurred at Stations 8 and 9, and in both places a few *Pectis* and *Bouteloua* germinated

(about 5-10 per m.^{2}). They flowered and set seed, even though the plants remained very small. At Station 11, in that same summer, no rain occurred, but on a nearby slope precipitation was barely sufficient to have some water stream down a few washes. There a few seedlings germinated, but there was not enough water on the soil to carry them through, and consequently they died before flowering.

After the winter rains, the amount of germination was proportional to the amount of precipitation. The first rain of the winter season had to be well over 10 mm., preferably 20 mm. or more, before germination would occur. Also, the night temperature had to remain at or above freezing. Heavy rains or snow at lower temperatures were ineffective in causing germination. When the first rains were accompanied by moderate temperatures but were of only 10 mm., another rain of 10 mm. or more would be required to bring about further germination.

If, however, the first rains were accompanied by very low temperatures, a subsequent rain of as little as 5 mm. could result in germination. This could be explained by assuming that a germination inhibitor is released by a rain of 10 mm. or more, but if the temperatures are not suitable for germination, the inhibitory factor is reconstituted again, so that another rain of 10 mm. or more is again required for germination. If, however, temperatures during and after the first rain are very low, the inhibitory factor is not reconstituted. Consequently, the seeds can germinate with much less rain, given suitable temperatures.

Once sufficient germination had taken place to produce a closed cover of plants, subsequent rains at various temperatures did not produce any further germination within the existing thick vegetation. In nearby areas where there was not a closed cover, more germination occurred. In soil samples taken from the thickly covered areas, further germination took place in the laboratory. Competition for moisture by the plants already germinated could hardly have been the reason for the non-appearance of new ones in the field, for the seedlings already up were small and by no means exhausted the soil moisture, nor did they create shade of an extent which could be limiting. The phenomenon is believed to be due to germination inhibition by an existing vegetation. This conclusion was first based on counts of seedlings and successive visits to the plots, and later confirmed by counts made from photographs. Further investigations are being carried out in the laboratory.

TABLE IV. Number of seedlings which germinated and number of surviving seedlings at various stations in the season of 1948-1949

Station	Elev. in meters	No. of seedlings Dec. 12	Mar. 13	Apr. 30	Identified species germinating at rates from 50 to 600 seedlings per m^2.
5.....	600	500	22	18	None identified
7a.....	670	2000	364	244	*Chorizanthe, Monoptilon*
7b.....	800	1000	128	62	*Chorizanthe, Salvia*
8a.....	900	500	—	251	*Cryptantha, Eriophyllum, Pectocarya*
8b.....	1100	1200	—	1008	*Cryptantha, Filago, Chorizanthe, Coreopsis, Eriophyllum*
6.....	1150	1500	3140	766	*Chaenactis, Coreopsis, Eriophyllum, Pectocarya*
8.....	1200	1000	—	966	*Bromus, Chaenactis, Erodium, Eriophyllum*
7.....	1220	1000	—	872	*Amsinckia, Chorizanthe, Eriogonum, Eriophyllum, Pectocarya*
9.....	1220	1000	—	512	*Chaenactis*
12.....	1300	200	64	93	*Eriophyllum, Gilia aurea, Gilia scopularum*
9a.....	1370	800	—	298	*Cryptantha, Eriophyllum*
10b.....	1370	2000	1450	1492	*Eriophyllum, Gilia aurea, Gilia scopularum, Pectocarya*

TABLE V. Typical survival figures, obtained in the season of 1951 and 1952. By means of 3-dimensional photographs, it was possible to tell that the plants surviving in April were the same individuals that germinated in February or March.

Station elevations (m)	Number germinating	Number surviving seedlings	% survival
600-800.....	3,500	324	9
900-1150.....	4,840	2,025	42
1200-1370.....	6,000	4,233	71
Total.....	14,340	6,582	46

Table IV shows the number of seedlings and plants counted on successive visits to the different plots during the 1948-49 season. On the average more than 50% of the plants which germinated survived and produced seed.

All observations support the thesis that most seeds of these desert annuals do not germinate unless the conditions for continued growth are favorable, and that most seedlings survive. Therefore, there is little selection occurring during the vegetative development of these annuals, which explains why most of them do not show special adaption in their vegetative characters to the desert habitat. Their adaptations have to be sought in their early maturation and in their germination characteristics.

SUMMARY

Twenty-three stations with rain gauges and quadrats of one square meter were set up in Joshua Tree National Monument. Over a 5 year period the germination of annuals was correlated

with precipitation and maximum-minimum temperatures.

Samples of soil were taken from each station, and placed on flats of sand in controlled climatic conditions in the Earhart Laboratory. Germinations were counted and seedlings grown to maturity and identified. Drawings of the cotyledons and first leaves of many of the species were prepared.

From the combined field and laboratory data, optimal conditions and critical extremes were determined for the species which germinated in quantity. It was found that temperatures which prevailed in a brief period following each rain, together with the amount and duration of precipitation, were the major factors that brought about germination, and that the total amount of germination was proportional to the amount of precipitation up to an optimum beyond which germination decreased. The amount of the first winter rain and the temperatures accompanying it were of especial significance. Leaching and wind were other factors of importance. Survival of the seedlings was also observed, and averaged over 50 per cent.

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NATURE OF THE PLANT COMMUNITY. I.UNIFORM GARDEN AND LIGHT PERIOD STUDIES OF FIVE GRASS TAXA IN NEBRASKA[1]

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The grassland type of vegetation approaches the ideal for an experimental analysis of the nature of the plant community. The growth form of most members of the grassland community, in contrast with those of communities in which woody members predominate, allows liberal use of transplant techniques. Readily available clones of most members at any time during the year afford ample material for an experimental study.

For an understanding of the nature of a plant community which has been geographically oriented and whose composition has been determined with respect to plant identification, the individual plant behavior within the community needs to be observed and evaluated. The present study was designed to observe individual behavior and then to compare the behavior of individuals of a number of species from one community site with individuals representing the same series of species from a different community site.

Uniform Garden Approach

While the vegetational composition varies considerably throughout Nebraska, a number of grasses occur widely in the state. When clones representing a number of these grass taxa were collected for the uniform garden study, there was an attempt to obtain samples widely throughout the state. At any particular community site, the individuals removed for transplanting represented some or all of the following taxa: *Bouteloua gracilis* (H.B.K.) Lag., *Bouteloua curtipendula* (Michx.) Torr., *Andropogon scoparius* Michx., *Andropogon gerardi* Vitman—*A. hallii* Hack. complex, and *Panicum virgatum L.* The majority of the clones were removed from the collection sites between July 24 and August 19, 1953. Certain collections of *P. virgatum* were removed on September 20. A piece of each clone was preserved as a documentation of the development under habitat conditions of 1953. The remaining part of the clone was tagged and was placed in a tub of moist Sphagnum moss. The clones were subsequently put into a spaced planting at Lincoln. At the time of planting, the cultivated soil was fairly dry and a technique of placing the clone into a pool of mud prior to covering with dry soil was used. There was no watering of the clones

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during the growing seasons of 1954 and 1955 when phenological notes were recorded.

Uniform Garden Results

(1) *Bouteloua gracilis*

From the accompanying map (Map 1 of Figure 1), it is apparent that the earliest flowering dates are for clones from the westernmost part of the state. A period of 36 days separates the earliest and the latest anthesis dates for clones in the uniform garden at Lincoln. All of the clones continued to produce new flowering culms, and there were culms in anthesis almost continuously on all clones until the last records were taken on August 15. During 1955, an early series of growing conditions placed the earliest flowering dates in May. Most of the dates during 1955 were approximately 2 weeks earlier than in 1954. The last clone to flower in 1954 (TH-108—July 17) was also the last to flower in 1955 (July 5).

(2) *Bouteloua curtipendula*

The first date of anthesis in the uniform garden varied among the different clones over a period of 50 days (Map 2 of Figure 1). The earliest clones to flower were from the westernmost part of the panhandle area. The earliest anthesis date was June 20. The later flowering types were from more easterly site and the last clone to flower (August 8) was from the southeastern corner of the state. Only a slight amount of variation was shown between 2 clones from the same site. Two clones from a population in the western part of the state were in anthesis on June 24 and June 26, respectively. Two clones from a site in the southeastern corner of the state flowered on July 19 and July 24, respectively. All of the clones continued to produce new flowering culms through the summer and were in anthesis on August 15. In 1955, a similar sequence of anthesis dates was observed. The dates recorded in 1955 were generally 2 weeks earlier than those recorded in 1954.

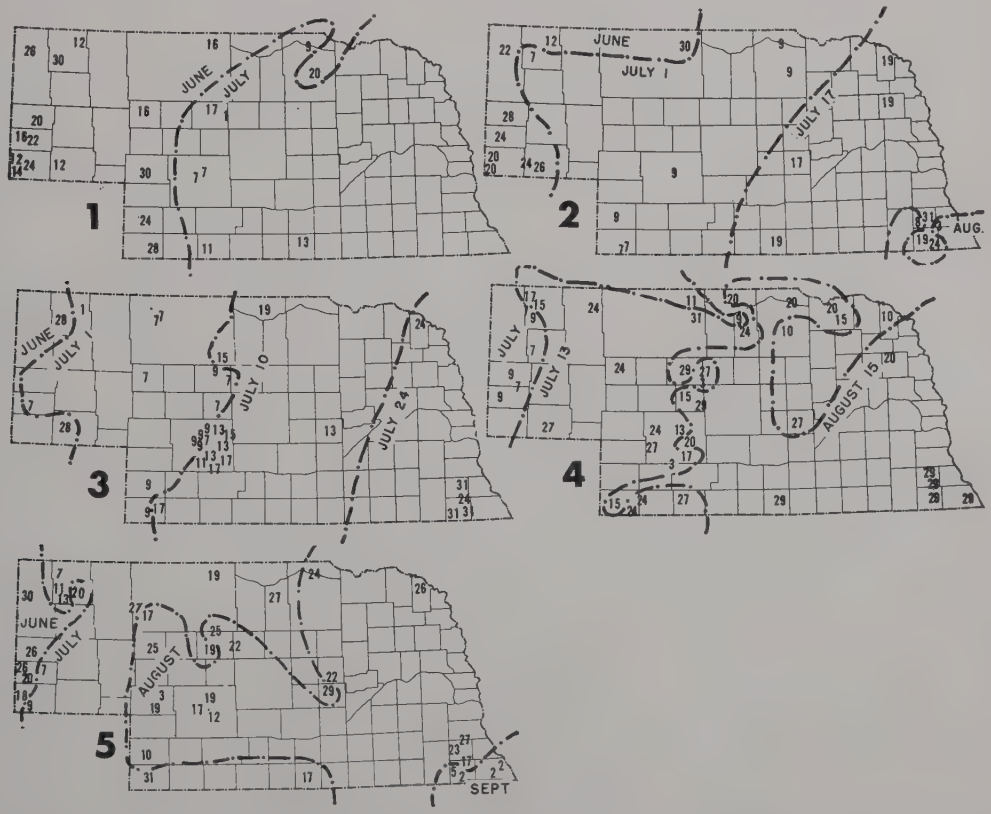


Fig. 1. Anthesis dates (1954) for clones in a uniform garden at Lincoln, Nebraska. Each map contains the anthesis dates for a particular taxon: 1) *Bouteloua gracilis*, 2) *B. curtipendula*, 3) *Panicum virgatum*, 4) *Andropogon gerardi-A. hallii* complex, 5) *A. scoparius*. The anthesis date is placed approximately at the collection site. Those dates between August 15 and 29 are approximations for *A. scoparius*. The lines were drawn arbitrarily to separate earlier and later dates of anthesis.

(3) *Panicum virgatum*

The period of 34 days during 1954 which separated the earliest flowering dates for clones from the western part of the state from the latest flowering dates from the southeastern part of the state is shown on Map 3 of Figure 1. Clone FR-55 and clone PO-10, both from western localities, were in anthesis before the end of June in both 1954 and 1955. The latest flowering clones from the southeastern part of the state reached anthesis one to two weeks later in 1955 than in 1954. Although extended into August during 1955, the sequence of flowering was approximately the same during both years.

A series of clones collected in the vicinity of North Platte produced their first flowers at Lincoln during the period of July 7-17 in 1954. None flowered as early as the western clones nor as late as the clones from the southeastern part of the state. There was no correlation shown between flowering date and habitat near North Platte. The clones collected on the sandhills north of town flowered at the same time the clones collected on the alkaline flood plain along the South Platte River. Clones collected from the same habitat at two different times (Sept. 20 and Aug. 6) did not vary greatly in their anthesis dates.

(4) *Andropogon gerardi-A. hallii* complex

As in the other taxa, the clones with the earliest flowering dates in 1954 were from the westernmost part of the panhandle (Map 4 of Figure 1). The dates indicate a trend of progressively later flowering toward the southeastern corner of the state.

Although a number of clones flowered after August 15 in 1954, there was just one clone to flower after that date during 1955. Of the 12 clones with late flowering dates in 1954 (Aug. 16-29), 8 were among the late flowering clones in 1955 (July 27-Aug. 5). Seven clones were in flower by June 29 in 1955. Five of these 7 clones flowered between July 7 and 11 during 1954.

The greatest difference of blooming dates among clones from the same population was shown in this complex. A pair of clones from a North Platte site flowered in Lincoln on July 13 and August 20, respectively. A corresponding contrast in flowering date is apparent in the voucher specimens of these two clones. On July 24, 1953, the earlier flowering clone was in anthesis at the collection site. On the same date, the later flowering clone had just begun to produce elongating stems at the collection site. Other pairs of clones showed a difference in blooming date which could be correlated with their behavior at the community site. Most of the pairs which displayed strikingly different behavior were from populations throughout the central part of the state.

(5) *Andropogon scoparius*

Clones from the westernmost part of the panhandle of Nebraska were the earlier flowering types. The earliest record during 1954 was the anthesis date (June 18) for a clone from the southwest corner of the panhandle near Pine Bluffs, Wyoming (Map 5 of Figure 1). A period of 80 days extended from that earliest date until the date of flowering (Sept. 5) for a clone from the southeastern corner of the state.

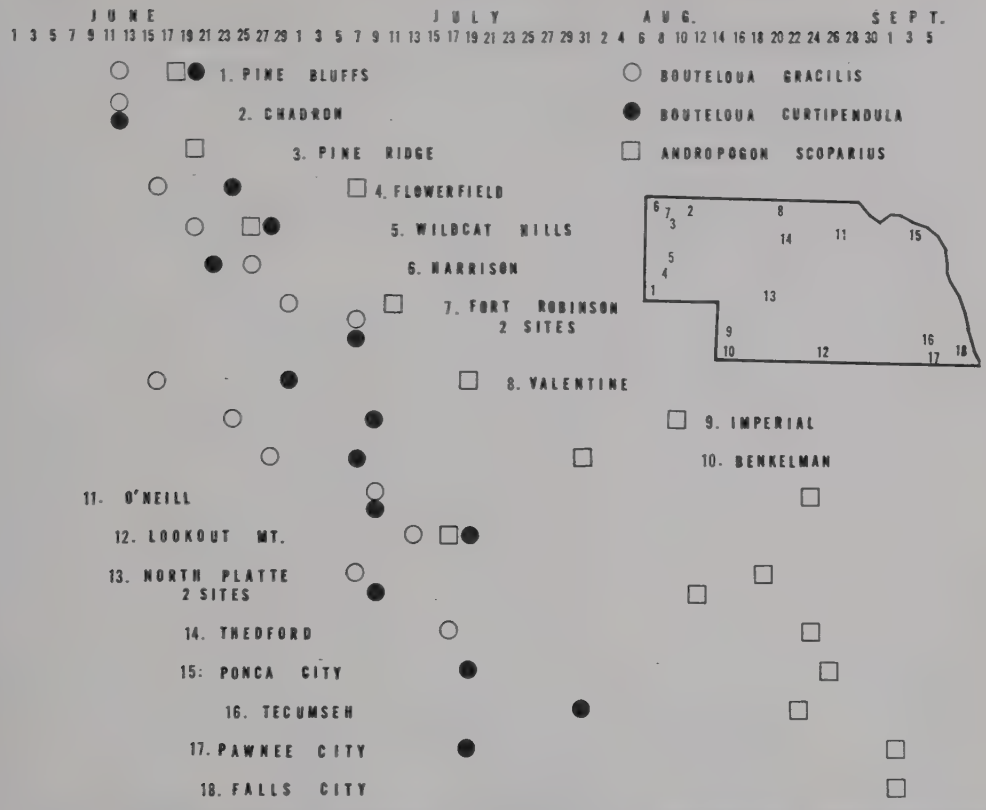
In 1955, a similar trend of flowering to that of 1954 was shown. The later clones from the southeastern part of the state flowered by August 18 during 1955 in contrast with flowering by September 2 during 1954. The clones with the earliest flowering dates in both 1954 and 1955 were from the panhandle area.

Comparison of Communities in the Uniform Garden

Some insight into the nature of the community can be attained by comparing the behavior of individuals representing the different taxa at a particular site. When the behavior of the clones representing *Bouteloua gracilis, B. curtipendula,* and *Andropogon scoparius* at the Pine Bluff locality in the panhandle are plotted together (Figure 2), it is apparent that all 3 taxa are represented by early flowering clones. A noticeable similarity in flowering date characterizes clones of the different taxa from the westernmost sites—Chadron, Pine Ridge, Flowerfield, Wildcat Hills, Harrison, and Fort Robinson. Clones from Lookout Mountain (central portion of the Nebraska-Kansas border) flowered at approximately the same time, but one month later than the Pine Bluffs clones. A greater difference in flowering dates is evident among the 3 taxa at the other sites located east of the panhandle (Valentine, O'Neill—north, Imperial, Benkelman—southwest, North Platte and Thedford—central). The northeast locality at Ponca City and the southeast localities (Tecumseh, Pawnee City, Falls City) display a wide separation of anthesis dates for the different taxa.

In mid-July, 1955, observations at several community sites in the western part of the panhandle revealed the almost simultaneous appearance of a first anthesis date for clones of all 3 taxa. In contrast, sites in the southeastern part of the state indicated a much earlier anthesis date for *Bouteloua* clones than for *Andropogon* clones.

When the flowering dates of clones of the *Andropogon gerardi-A. hallii* complex and of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1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 1 3 5
1. PINE BLUFFS
2. CHADRON
3. PINE RIDGE
4. FLOWERFIELD
5. WILDCAT HILLS
6. HARRISON
7. FORT ROBINSON 2 SITES
8. VALENTINE
9. IMPERIAL
10. BENKELMAN
11. O'NEILL
12. LOOKOUT MT.
13. NORTH PLATTE 2 SITES
14. THEDFORD
15. PONCA CITY
16. TECUMSEH
17. PAWNEE CITY
18. FALLS CITY
BOUTELOUA GRACILIS
BOUTELOUA CURTIPENDULA
ANDROPOGON SCOPARIUS

FIG. 2. Comparison of behavior of clones of *Bouteloua gracilis, B. curtipendula,* and *Andropogon scoparius* in a uniform garden at Lincoln, Nebraska. Each symbol indicates the first date of anthesis for a clone. Clones representing a particular community site are plotted horizontally.

Panicum virgatum are compared with those of the 3 taxa above, the width of the separation of the first anthesis dates at any site (Figure 2) remain unchanged or change but slightly. The *A. gerardi-A. hallii* clones showed a tendency to be earlier flowering than the *A. scoparius* clones from the same community site. In 15 community sites in which *A. scoparius* and *A. gerardi-A. hallii* were represented, *A. scoparius* was earlier in 3 (Pine Ridge, Wildcat Hills, Lookout Mountain). Flowering was recorded on approximately the same date for clones of the 2 taxa in 4 community sites. Clones of *A. gerardi-A. hallii* were earlier flowering in the remaining 8 community sites. In all 15 community sites in which *P. virgatum* occurred with either *A. scoparius* or *A. gerardi-A. hallii* or both, the *P. virgatum* clone was the earliest flowering of the 3 taxa. In the 13 community sites in which *B. gracilis* and *B. curtipendula* were growing together, the *B. gracilis* clones were earlier flowering by 8-20 days from 10 sites; the *B. gracilis* clone was later flowering at one site; and both kinds of clones from the remaining two sites were flowering at the same time.

A phenological sequence of the clones representing the 5 taxa from a particular site took the following general progression when grown in the uniform garden at Lincoln: *B. gracilis, B. curtipendula, P. virgatum, A. gerardi-A. hallii,* and *A. scoparius.* Six clones from a western site (near Pine Bluffs, Wyo.) showed this order of flowering: *B. gracilis*—June 12, June 14; *B. curtipendula*—June 20, June 20; *A. scoparious*—July 9, July 18. The 7 clones representing the Pawnee City site in the southeastern part of the state showed the following sequence: *B. curtipendula*—July 19, July 24; *P. virgatum*—July 31, July 31; *A. gerardi-A. hallii* complex—Aug. 29 (*i.e.,* 15-29); and *A. scoparius*—Sept. 2, Sept. 5. There is undoubtedly a certain amount of variation within each species-population at any community site. The actual progression in the uniform garden will depend upon the individuals which are selected to represent the population.

Light Period Studies

Clones from 5 of the community sites were removed from the field planting prior to the summer of 1954 and placed under greenhouse conditions. The 5 sites were selected from the group in the uniform garden because they each represented an area in which *B. gracilis, B. curtipendula,* and *A. scoparius* were growing together. The effect of different light periods on the clones was determined to see if part of the variation in behavior within each of the taxa could be correlated with a latitudinal position within the state.

The community sites were geographically located as follows: western panhandle—5 miles west of Harrisburg, Banner County, 20 miles northeast of Harrison, Sioux County; western central—Kingsley Dam, Keith County; northeastern—9 miles south of Niobrara, Knox County; and southeastern—9 miles northwest of Lincoln, Lancaster County. The location at Harrisburg (designated as HA) was in a large grazed pasture. The clones were removed from an eroded slope within the pasture. At Harrison (HR), the 3 clones were on a rocky slope. The Harrison locality was several miles to the north of Pine Ridge. At Kingsley Dam (KD), the 3 clones were dug on a rocky slope below a limestone outcropping. The site had frequent individuals of *Juniperus virginiana* L. and is just southeast of the dam. The clones at Niobrara (NI) were from the top of a sandy ridge above the Verdigre River. Adjacent slopes were covered primarily by individuals of *Quercus macrocarpa* Michx. The Lincoln clones (LI) were in a large unmowed, unplowed, grazed area known locally as Black's Pasture. The clones were from near the top of a rounded ridge with a fairly shallow loess mantle over glacial till.

The clones from the various localities except Lincoln were removed during the later part of July and August as mentioned in the uniform garden study. The Lincoln clones were removed from the collection site on February 5, 1954. All clones were dormant at the time of planting. Each clone was divided into 8 pieces of approximately

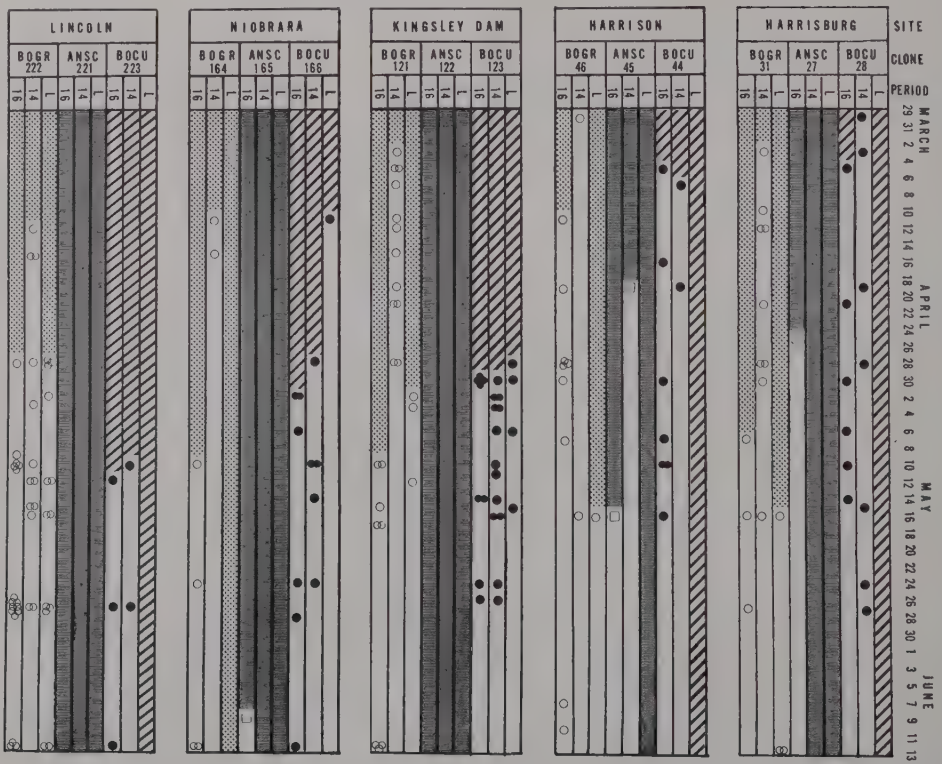

FIG. 3. Light period effects on clones from 5 community sites in Nebraska. The 3 light periods are increasing light period at Lincoln, Nebraska (L), 14 hour periods, and 16 hour periods. Symbols for *Bouteloua curtipendula* (BOCU) and *B. gracilis* (BOGR) indicate date of emergence of an inflorescence. Symbol for *Andropogon scoparius* (ANSC) indicates the anthesis date. Shaded portion is prior to emergence or anthesis.

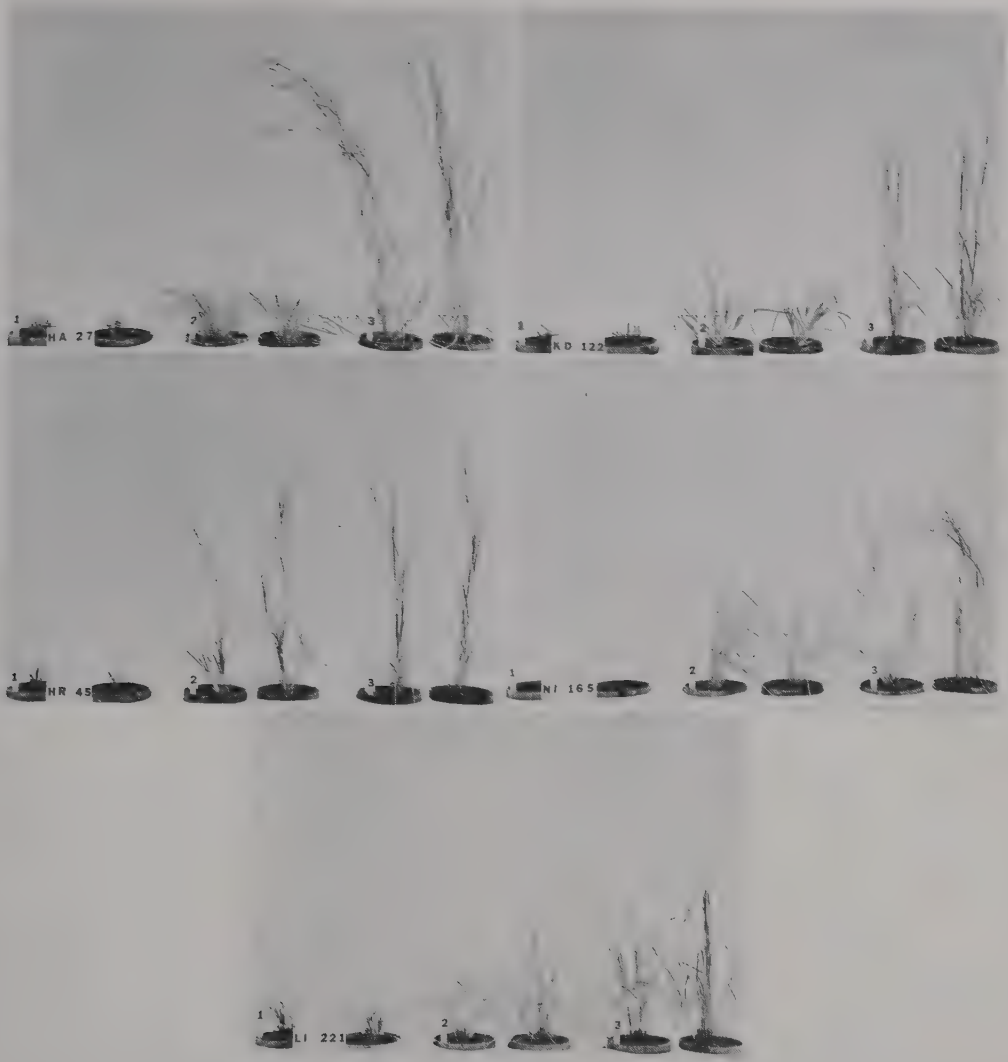

FIG. 4. *Andropogon scoparius* clones from 5 community sites, Harrisburg (HA27), Harrison (HR45), Kingsley Dam (KD122), Niobrara (NI165), and Lincoln (LI221) which were grown under 3 light periods: 1) increasing light period in Lincoln, Nebr., 2) 14 hour light periods, and 3) 16 hour light periods. Duplicate pieces of each clone under the various treatments photographed on May 17, 1954.

equal size. Each piece was planted in a 5-inch pot using a mixture of 3 parts loam to 2 parts sand. Two pieces of each clone were placed in each of 3 light period conditions: constant 14 hour light periods, constant 16 hour light periods, and regular increasing light periods at Lincoln, Nebraska. Two additional pieces were maintained under regular daylength conditions for substitution in case of growth failure. At the beginning of the study, the 14 and the 16 hour periods were merely extensions of the daylength. As the daylengths at Lincoln approached 14 hours, the tables were shielded by movable plywood covers in addition to heavy black canvas curtains.

The approach (Figures 3 and 4) used in this light period study does enable some estimation to be made of the responses to a controlled habitat of genetically distinct individuals in one plant community site when compared with their genetic counterparts from other plant community sites. This type of study might be termed a systematic physiological approach to the study of a plant community. An expansion of the study could involve either the inclusion of representatives from

a greater number of distinct genetic lineages or the inclusion of greater numbers of individuals representing the different populations comprising the plant community. Studies on the nature of certain grass populations from the comparative physiological approach will be discussed in a subsequent report.

Response of clones of Andropogon scoparius to light period

Ansc-HA-27.—The first clone to produce flowering culms in the light period study was one representing *A. scoparius* from the Harrisburg locality (Fig. 3). Anthesis occurred on April 25 under 16 hour periods. There was no elongation of stems under the 14 hour light period or the regular increasing light period conditions by June 12. Under habitat conditions at Harrisburg in 1953, this clone produced yellowish-green leaves which were comparatively short. In the greenhouse, the Harrisburg clone was conspicuously different from the other clones in respect to color and length of leaves. This clone was grown in the uniform garden and was one of the earliest flowering clones, producing flowers on June 26. A second clone from the same site produced its first flowers on June 20.

Ansc-HR-45.—The first flowering culms to be produced by the Harrison clone were those under the 14 hour light periods (April 19). These culms were produced during the same period that culms were elongating on the Harrisburg clone (HA-27) under the 16 hour treatment. Flowering culms were also produced by the Harrison clone under 16 hour light period conditions. Anthesis occurred on May 16. No elongating stems appeared on the pieces of the clone under increasing daylengths.

Ansc-KD-122.—Well-developed stems were evident on the Kingsley Dam clone under the 16 hour light period conditions by May 16 (Fig. 4) the date of first anthesis by the Harrison clone. Rapidly elongating culms appeared under the 14 hour conditions subsequent to their production under the 16 hour conditions, but anthesis had not occurred by June 12. A portion of the Kingsley Dam clone which was maintained in the uniform garden began elongating culms on July 1, 1954. Anthesis occurred on August 3. Under similar garden conditions, the Harrisburg material was in anthesis by June 26.

Ansc-NI-165.—There were no elongating stems produced by this clone under either the 14 hour conditions or the increasing light period conditions. Under the 16 hour light period, flowering culms were evident, anthesis first occurring on June 9.

Ansc-LI-221.—There were no elongating culms evident on clonal members of the Lincoln material at the time of flowering of the Harrisburg clone (Fig. 4). Subsequently, elongating culms were first produced on the 16 hour light period conditions and later appeared under the 14 hour conditions. The tallest culms on the Lincoln clone were shorter than the tallest culms of any other *A. scoparius* clone on June 12. This was the only clone which neither flowered nor had emergence of the inflorescence from the sheath.

From the work of Larsen (1947) and Cornelius (1947) it is apparent that the wide-ranging taxon, *Andropogon scoparius,* is characterized by ecotypic variation. Cornelius found variation among 16 strains from a broad geographic area when grown from seed at Manhattan, Kansas. He found that the northern strains (North Dakota and Wyoming) flowered in late June at Manhattan. The southern one (Texas and North Carolina) did not flower until September or October. The strain from Cheyenne, Wyoming, which Cornelius studied was one of the earliest flowering strains. The Cheyenne strain is from a geographic area adjacent to the Harrisburg locality of the present study. The O'Neill strain used by Cornelius is from northeastern Nebraska near the Niobrara locality of this study. The O'Neill strain was one of the earlier flowering strains used by Cornelius, although it flowered almost a month later than the Cheyenne material. In a similar fashion, the Harrisburg material flowered approximately a month and one-half earlier than the Niobrara clone in the present study.

Larsen used 40 clones from 12 widely separated areas in the United States. None of the collection sites was in Nebraska, but the Cheyenne, Wyoming, site and the Manhattan, Kansas, location are in adjacent areas. In Larsen's study, neither the Kansas clone nor the Wyoming clone flowered under 14 hour light periods; however, both clones flowered under 15 hour periods. In a similar manner, in the present study, both the Harrisburg and the Niobrara clones failed to produce elongated culms under the 14 hour conditions. However, the Harrison clone from a more northerly geographic position than either the Harrisburg or the Cheyenne material flowered under the 14 hour conditions. Both the Lincoln and the Kingsley Dam material which were from more southerly positions than the Niobrara clone produced elongated culms under both 14 and 16 hour conditions although actual flowering had not occurred by June 12. While it is not possible to compare the results of the present study directly with that of Larsen, it would appear that the greater the num-

ber of clones which are taken from within a restricted geographic range, the more apparent will be the variation within the species. Variation which might appear to be clinal or ecoclinal by one sampling technique is apt to be complicated by additional samples.

From the present study of the 5 clones of *Andropogon scoparius* in Nebraska, one might conclude that flowering is earlier in western clones. The different responses of the Harrisburg and the Harrison clones to the same light periods do not allow a correlation of flowering behavior with latitude and length of light period. Present studies being conducted on populations of *Andropogon scoparius* from a number of community sites should provide further information.

Responses of Bouteloua curtipendula to light period

Bocu-HA-28.—The clone from Harrisburg was the earliest to produce flowering culms (Fig. 3). The first culm appeared on March 30 under the 14-hour treatment. Emergence began on April 5 under the 16 hour conditions. There were no culms produced under the increasing light periods.

Bocu-HR-44.—Flowering culms appeared almost simultaneously on the 14 and the 16 hour light periods. As in the case of the Harrisburg clone, no flowering appeared under regular daylengths.

Bocu-KD-123.—Flowering culms appeared under all 3 light period conditions almost simultaneously. This clone differed from the 2 western clones in producing flowering culms under the increasing light period in late April.

Bocu-NI-166.—The earliest emergence of a flowering culm on this clone was under the increasing light periods. Flowering culms were produced on both the 14 and the 16 hour light periods.

Bocu-LI-223.—The Lincoln clone was the latest flowering one representing this species. The flowering culms were evident on May 10 and 12 on the 14 hour and the 16 hour light periods, respectively. The Lincoln clone was the last to begin growth after being placed in the greenhouse where it continued to grow very slowly under all treatments.

A number of other clones of *B. curtipendula* from the Lincoln collection site were grown under 13, 14, 15, and 16 hour light periods. Most of these clones flowered under 14, 15, and 16 hour conditions. A few flowered under the 13 hour periods. Striking differences were apparent, however, between certain clones, as exemplified by one clone which flowered only under 16 hour light periods and another clone which failed to flower under any of the light periods.

The variation in response of clones of *Bouteloua curtipendula* to the 14 and 16 hour light periods was largely one of earliness of flowering, since all clones produced flowering culms under the 2 treatments. There was a difference in flowering under increasing light periods. Only the Kingsley Dam and the Niobrara clones flowered under natural daylengths by June 12.

The earliest production of flowering culms was shown by the 2 westernmost clones (HA-28 and HR-44). The more southerly of the 2 clones, the Harrisburg one, flowered almost equally under the 14 and 16 hour periods. In contrast, the Harrison clone had a very short flowering period under the 14 hour light periods. The Kingsley Dam clone was intermediate in earliness, and the Niobrara and Lincoln clones from the eastern part of the state were the latest flowering clones.

Three Nebraska strains of *B. curtipendula* were included by Olmsted (1944) in a study of the response of 12 geographical strains to varying light periods. None of the 3 strains flowered under 13 hour light periods, whereas all of the 3 strains flowered under 16 and 20 hour periods. The 3 strains were from a north-south transect through Nebraska which would include approximately the Niobrara and Lincoln localities of the present study. The 3 strains, as studied by Olmsted, varied slightly from each other in flowering behavior, resembling each other in this respect, however, more than they did the behavior of the more southern strains which flowered under a 13 hour light period.

Again the question could be raised concerning the behavior of the individuals comprising a population. Certainly one clone could not be expected to duplicate the behavior of all of the individuals in a population except perhaps in the case of a completely apomictic one. The breadth of the variation of response within a population remains to be more fully studied.

Responses of clones of Bouteloua gracilis to light period

Bogr-HA-31.—Early flowering under 14 hour light periods was observed in the Harrisburg clone (Fig. 3). There was very little difference in the vegetative growth of the clone under the 3 light period treatments. The chief difference among the 3 treatments was in time of emergence of flowering culms and in number of flowering culms.

Bogr-HR-46.—The Harrison clone was the earliest flowering clone under the 16 hour periods.

Conspicuously, the least growth had taken place on this clone under regular days prior to March 26 in contrast to equal growth which was apparent on the 3 treatments in the case of the Harrisburg clone. The more northern of the 2 western clones, HR-46, had a longer flowering period under 16 hour periods, whereas the more southern clone, HA-31, seemed to be better adjusted to the 14 hour periods.

Bogr-KD-121.—The Kingsley Dam clone flowered under the 3 light period treatments, the flowering culms appearing approximately 5 weeks earlier under the 14 hour light period than under the 16 hour light period.

Bogr-NI-164.—The Niobrara clone was the only *B. gracilis* clone which failed to produce at least one flowering culm under the regular increasing daylengths by June 12. It produced an early but short flowering period under 14 hour treatments and later but longer flowering under 16 hour treatments.

Bogr-LI-222.—Although flowering was slightly earlier in this clone under 14 hour light periods than under 16 hour light periods, the subsequent flowering under both the increasing light periods and the 16 hour light periods gave a strikingly similar appearance under the three treatments. In number and length of flowering culms and in flowering period, the clonal pieces were more similar than were the pieces of any other clone in the study.

Riegel (1940) grew *Bouteloua gracilis* from 9 sources at Fort Hays, Kansas, in 1938 and 1939. The Nebraska strain which was included in the studies was in anthesis 3 weeks later than the Wyoming and Colorado strains. While the exact source of the strains is not cited by Riegel, the Nebraska strain might have come from the eastern part of the state, since in flowering the western collections of the present study have been more like the Wyoming and Colorado strains used by Riegel.

The westernmost clones of *B. gracilis* were the earliest flowering under the 14 hour light periods of the 5 included in the present study. The 2 eastern clones, NI-164 and LI-222, were only slightly later in flowering under the 14 hour periods. All of the clones were considerably later flowering under 16 hour periods than under 14 hour periods.

Comparison of Community Sites under Varying Light Periods

In this comparative approach to the study of a plant community, three evaluations can be made: first, an evaluation of the flowering behavior of different individuals of the same taxa; second, an evaluation of these individuals as they represent the members of a plant community; and third, an evaluation of a number of community sites containing genetic counterparts within the vegetation of Nebraska.

The individuals have been dealt with in regard to variation within the taxa they represent. In order to deal with the plant community, the individual must be compared with the other individuals from the same community site. It was demonstrated that the 3 individuals representing 3 different genetic lineages as they grew together at Harrisburg did not respond to the 3 light periods identically. The 3 members of any of the 5 community sites studied could be analyzed similarly. It is fairly obvious that each individual responds to its environment as a result of its own genetically-controlled physiological tolerances. That 3 genetically-diverse individuals would present identical behavior patterns to a controlled habitat is quite unlikely. The spatial arrangement of the individuals within a plant community has been selected by an intricately patterned habitat. Natural selection has yielded groupings which are in adjustment with the habitat, but the grouping will exist only to the degree that the environment of each individual allows its survival.

The 3 individuals from Harrisburg, when compared with their genetic counterparts from the Harrison locality, approximately 100 miles to the north, indicate an earliness of flowering for the 2 *Bouteloua* members, but a strikingly different behavior for the *Andropogon* member. When compared with the other three communities, the 2 western ones are more like each other than they are to those approximately 400 miles to the east. The comparison of clones from community sites under light periods lends itself to a conclusion similar to that reached when comparing the communities under the uniform garden treatment. The occurrence of the 3 taxa together in a number of areas should provide no safe criterion for judging the habitats to be the same in all cases. Early flowering types of any number of genetic lineages might be selected out in one habitat and later flowering types of the same genetic lineages might be selected out in another habitat. While the composition in terms of taxa represented may remain constant, the actual genetic composition of the vegetation can be vastly different.

Discussion

The individualistic concept of the plant community as proposed by Gleason (1926) and as expanded by Mason (1947) and Cain (1947) has been dealt with recently by a number of ecological workers. Billings (1949), in examining the geo-

graphic ranges of 7 shrubby species which grew together in western Nevada, noted that all but one species extended far beyond the typical shadscale vegetation of that area. The area of overlap of the 7 taxa was relatively small, and Billings suggested that the overlap results from the coincidence of environmental requirements of the component taxa in that part of their respective ranges. He suggested that his evidence led him to agree with the individualistic concept of the plant community. Whittaker (1951, 1952) has expressed confidence in the individualistic concept on the basis of distributional patterns which were charted for 100 taxa. He found no two patterns to be alike. Whittaker suggested that the individualistic concept applies to the animal community as a result of his investigation of insect distribution in the Great Smoky Mountains. Curtis and McIntosh (1951) and Brown and Curtis (1952), dealing with distributional patterns, have suggested that their continuum analysis substantiates the individualistic concept as presented by Gleason.

Seemingly, the individualistic concept has gained its support, most of which is fairly recent, from studies of vegetational composition. In these studies, the recognition of different groupings of taxa has been the basis for the evaluation. In the present study an attempt has been made to keep the grouping of taxa as nearly an experimental constant as possible. It would not be difficult to further document this study with comparisons of the distributional patterns of the taxa involved. In no case would one find that the grass taxa dealt with in the present study would have a complete coincidence in restricted distribution within Nebraska or in total distribution.

The present experimental analysis indicates that the overlapping of the distributional patterns of the various taxa involves the overlapping of ecotypic variation within the taxa. The results of this study augment other studies that the indicator value of the species for habitat conditions is restricted to local application. The study further indicates that a grouping of species may be only of local value in the determination of habitat conditions.

The transplant work of Clausen, Keck, and Hiesey (1940) involved a number of taxa which were distributed at various altitudes along a transect of the Sierra Nevada in California. The results of their studies indicate that the individuals representing a number of taxa, growing at a similar altitude but not necessarily together in a community arrangement, had certain behavior patterns in common. Since the approach used by Clausen, Keck, and Hiesey was for the determination of variation which characterized individuals and populations, the community analysis was not included in their investigations. It would appear, however, that the results of the present studies bear a resemblance to the results of their investigations.

The tendency to consider a "grassland climate" and a "grassland soil" as a unit has minimized the striking habitat differences which exist both latitudinally and altitudinally within Nebraska (and in the Midwest, in general). While altitude, *per se,* is in itself not an explanation of habitat variation, its interaction with latitude and longitude does allow an evaluation of the selective forces acting upon the grassland vegetation.

A number of climatic patterns can be superimposed upon the altitudinal gradient within the state (ca. 900 feet in the southeast to ca. 5,000 feet in the west). Many of the climatic patterns (Visher 1954) tend to cross the state from northwest to southeast, some of these being: late spring frost probability, early fall frost probability, daily minimum temperature, normal date of beginning of distinctly dry season (2 months earlier in west than in east), average length of relatively dry season (8 to 10 months in west and 2 to 5 months in east), average length of wet season, normal date of first snowfall, percentage of normal annual precipitation as snow, normal spring precipitation, normal summer precipitation, normal fall precipitation, normal winter precipitation.

Apparently the recurrence and the concomitance of a number of climatic patterns over the state of Nebraska have selected out genetic types within a number of species for survival under the prevailing habitat conditions. An individual plant which has the ability to grow rapidly and to flower early would seemingly be favored in the western areas with a probability of late spring frost, early dry season, short wet season, low rainfall, and early fall frost. There has apparently been a selection of individuals of this type in a number of widespread grass taxa.

In the southeastern part of the state, the high probability of a long growing season does not exert the same sequence of climatic selective pressures which prevail in the more westerly sites. In the southeast, the position of each species-population within the phenological progression at a particular community site appears to be genetically fixed. Some shifting in the phenological progression is possible from one year to the next due to modifications induced by annual variations in the habitat conditions. At any community site, the probability of a sequence of habitat conditions has selected out a particular genetic lineage for

growth and maturation during a particular part of the long growing period.

The genetically-determined rate for reaching maturity under a given light period is more critical in explaining the difference in flowering behavior of clones from various community sites than modifications produced under different light periods. Most of the clones which were observed in 14 and 16 hour light periods were not greatly affected in their blooming behavior. Most of the period between the latest and earliest killing frosts in Nebraska lies within the 14 to 16 hour day-length range. It is possible that length of light period accompanied by different sequences of night and day temperatures would have produced different behavior by clones from different parts of the state.

Selection occurring independently in all parts of the state has resulted in the existing combinations of ecotypic variants within a number of widespread species. With the continued reduction of the number of grassland areas in Nebraska (and in the Midwest, in general), the availability of genetic lineages for maintenance of grassland vegetation in a multitude of habitats is being seriously depleted. In order to maintain the grassland type of vegetation with its present species-components, it is apparent that many areas must be maintained throughout its latitudinal and longitudinal distribution, so that much of the reserve of genetic variation within the taxa of the North American grasslands will not be lost for future generations.

Summary

Clones representing 5 grass taxa were grown in a uniform garden at Lincoln, Nebraska. In each of the taxa—*Bouteloua gracilis, B. curtipendula, Panicum virgatum, Andropogon scoparius,* and the *A. gerardi-A. hallii* complex—the earliest flowering clones were from the western part of the state. Clones from progressively more eastern localities exhibited a tendency to flower at progressively later dates. The community sites in the southeastern part of the state contained the later flowering clones of all taxa represented.

Clones of *B. gracilis, B. curtipendula* and *A. scoparius* from 5 geographically distinct community sites were grown under 14 hour, 16 hour, and regular increasing light periods at Lincoln, Nebraska from February to June. Clones from each of the 5 sites presented a different series of responses. The western material was earlier flowering, and the eastern material was later flowering, as in the uniform garden.

The probability of a sequence involving late spring frosts, short wet season, early beginning date of dry season and early fall frosts in the western sites has selected out individuals for rapid growth and early flowering in a number of different genetic lineages. The sequence of habitat conditions in the southeastern part of the state has been conducive to the selection of different genetic lineages in a phenological progression through a relatively long growing season.

It was concluded that the occurrence of the same series of taxa together at different sites does not afford a safe criterion for judging the habitats to be the same. In any particular habitat of the grassland community, there has been a selection of ecotypic variants within a number of different taxa for conditions which exist at that site.

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VASCULAR VEGETATION OF A RECENT VOLCANIC AREA IN NEW MEXICO[1]

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INTRODUCTION

The two adjacent lava beds at Carrizozo, New Mexico, known locally as the *malpais,* the Spanish term for badlands, lie in the northern part of the Tularosa Basin, an internal drainage area of approximately 6,000 square miles. The smaller, earlier flow, roughly triangular in outline and covering about 25 square miles to the northwest of the recent lava bed, was erupted during the Pleistocene (Meinzer and Hare 1915). The more recent volcanic deposit is estimated to have been extruded within the past 1,000 years (Allen 1951) from a small cone at the nothern end and possibly from other cones now buried.

The present paper (a) considers the distribution of vascular vegetation in relation to the several types of habitats within the younger lava flow, as well as to altitude, and (b) compares the vegetation of this recent volcanic deposit to that of other parts of the surrounding Tularosa Basin with respect to diversity of species. This work was done as a preliminary to making analyses for micro-Kjeldahl amino leaf nitrogen of the more prominent species and determinations of soil nitrite and nitrate.

A lava flow in Mexico, which received an annual precipitation of around 27 inches, was revegetated within 45 years after cooling to the point that it would support seed plants (Gadow 1930). Another, in the Belgian Congo, with an annual precipitation of 15 inches, was reclaimed by ferns in the crevices and more than 20 species of xeric seed plants within 13 to 18 years (Robyns 1932).

The earliest published reference to the vegetation of the Carrizozo malpais was Tarr's brief statement (1891) about the meagerness of the flora. Approximately a half century later, Benson (1933), Dice (1940), and Blair (1943), making observations independently on the mammals within the area, contributed substantially to an understanding of the general region and referred to certain plant species as elements of particular associations.

The older deposit, now nearly concealed by soil, is revegetated to the point that except for a cover of junipers it is almost indistinguishable from the surrounding plain, and the basalt rock, where exposed, is much weathered (Fig. 1). However, on the younger lava bed which, viewed from either side, forms a slaggy black stripe down the gray-brown of the alkaline plain (Fig. 2), plant growth is largely confined to scattering surface pockets and deeper crevices. The retarded development of a soil and vegetative cover on this more recent volcanic deposit is attributable mainly to the aridity, the short growing season, and the elevation of the flow above the surrounding area.

FIG. 1. Vegetation and exposed weathered lava on smaller, older lava bed (Pleistocene).

PHYSIOGRAPHY AND CLIMATE

The younger volcanic deposit filled a narrow valley approximately 44 miles in length and from ½ to 5 miles wide (Fig. 3). It followed a large arroyo along the main axis of the basin, also blocking tributary streams at present represented on either side of the malpais by shallow depressions which retain water for a time after heavy rains. The lava ranges in thickness from a maximum depth of 70 feet, indicated by a hole near the cen-

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FIG. 2. Sink-hole and barren lava surface typical of most of the Carrizozo lava bed.

ter (Allen 1951), to 10 to 20 feet along the margin. The original surface crust frequently broke from its own weight, forming irregular masses which were left inclined in all directions as the mass solidified. Black lava blocks, which may absorb enough heat during the summer days to remain warm overnight, adjoin shaded crevices and sink-holes which efficiently collect and retain both soil and moisture, providing a more favorable habitat for vegetation than the non-lava land of the surrounding area.

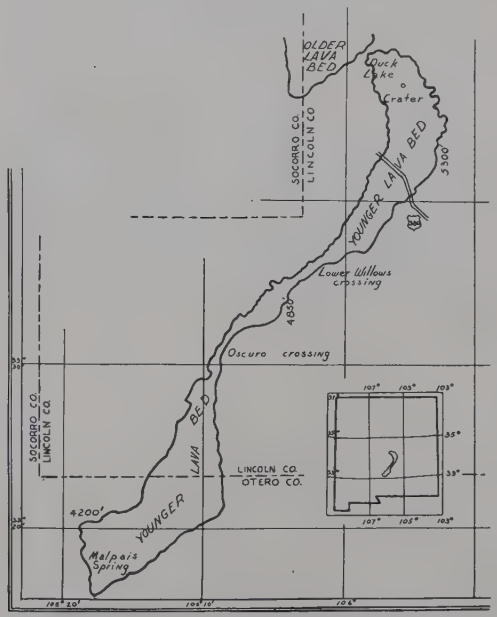

FIG. 3. Outline and position in New Mexico of the Carrizozo lava flow, ½ to 5 miles wide and 44 miles long.

Water which percolates through steam blebs in basalt rock dissolves out some of the mineral constituents, which usually are deposited in the cavities. As a rule, soil derived from igneous formations is finer and looser than that from sedimentary rock (Carter and Cory 1931) and has a characteristic red-brown coloration. The recent Carrizozo lava, however, has been little affected by the elements, soil formation and accumulation proceeding slowly and apparently gaining momentum only in recent years.

The water table, in places at least, is nearer the surface within the malpais than on the adjacent plain. On one small hill surrounded by lava and left as an island or *kipouka,* the water stands within 6 feet of the surface, compared to a water table 15 to 70 feet deep on the east side of the lava bed and 50 to several hundred feet deep on the west side.

A mile and a half to the northwest of the southern tip of the flow, water escapes from the margin as the gypseous Malpais Spring.

The typically low rainfall and moderately high

temperature of the southwest characterize this general area. Approximately the northern two-thirds of the lava flow lies within the Upper Sonoran and the southern third in the Lower Sonoran Zone. Variations in precipitation along the length of the deposit are correlated with a range in altitude from 4,100 feet at the southern tip to 5,360 feet at the northern extremity. At Carrizozo, which is 3½ miles east of the malpais about 10 miles north of the midline, the average annual precipitation over a period of 22 years was 11.37 inches, 8.40 of which fell during the growing season from April through October (U.S.D.A. Weather Bureau Climatic Summary of U. S., Section 29). The average annual precipitation about 20 miles below the southern tip is less than 9 inches, 5.4 of which falls during the rainy season in July and August (Shields 1953).

Method

The list of plant species occurring in the recent Carrizozo volcanic deposit was compiled from collections made in 42 field days, half of which were in June and the rest of which were distributed about equally in late April and August and in early November. Specimens were taken from 5 representative 100-yard wide belt transects across the lava bed; from one strip 6 miles long parallel to the length toward the center of the flow immediately west of Carrizozo; on two trips to the crater; and on two hikes around the greater part of the margin of the flow. Field notes covered the distribution of the more representative species within the lava flow, on the surrounding alkaline plain, and on the nearby Alamogordo gypsum deposit where several studies have been conducted during the past 5 years. Herbarium specimens of the plants collected are deposited at New Mexico Highlands University.

Observations and Discussion

Within the Carrizozo lava flow, 4 specific types of plant habitats exist: (a) the outspread basalt surfaces, constituting the greater portion of the malpais; (b) the major depressions, consisting of crevices or sink-holes resulting from collapsed basalt roofs; (c) two or more *kipoukas;* and (d) the loose cinders lining the crater and forming the outer slopes of the cone. These several environments influence plant life chiefly through differences in soil depth and variations in humidity and soil moisture.

The relative abundance of the various species within each of these habitats can be designated by one of the following symbols, which are employed in the distribution lists given later:

f—frequent, but scattered, a few visible from any spot in that particular section of the lava;

o—occasional, widely scattered, visible from only a few places;

r—rare, encountered in only a few locations where three to several individuals grew; and

1, 2, 3, 4, etc.—the total number of specimens observed.

Upper and Lower Sonoran Zone vegetation within the recent lava flow

The increase of more than 1,200 feet in elevation and of around 3 inches in average annual precipitation along the 44 miles between the southern and nothern extremities of the volcanic deposit are important factors influencing species zonation and density of growth. Further, the more shallow lava of the southern third of the flow lacks the deep, sheltered crevices especially characteristic of the northern half lying around and below the crater.

The distribution of observed species, exclusive of grasses, between the Upper and Lower Sonoran Zones within the lava can be shown most readily in tabular form:

a. Upper Sonoran Zone only (northern half of lava)	85
b. Lower Sonoran Zone only (southern third of lava)	14
c. common to both zones within lava	14
d. in overlap zone only	1
Total species, exclusive of grasses, in lava proper	114

Certain species characteristic of each zone extend into the overlap area between the northern half and the southern third. The better development of the vegetative cover on that part of the malpais within the Upper Sonoran Zone is evidenced by the 99 species, exclusive of grasses, found to grow on the northern half of the lava compared to 28 species occurring in diminished density on the southern third. At the higher altitude toward the northern tip, the surface is forested by *Juniperus monosperma* (Englem.) Sarg. which extends along the several tongues of the old lava bed, outlining the basaltic rock even where it does not break completely through the soil. Within the lava, *J. monosperma* extends to a point 10 miles below Carrizozo, which is farther southward and to a lower elevation than this species occurs in the surrounding area. At this point, along the Lower Willows crossing over the bare bedrock, the brief overlap of the Upper and Lower Sonoran Zone vegetation can be observed, the southernmost *J. monosperma,* an indicator of the Upper Sonoran Zone, appearing among a scatter-

ing growth of two indicators of the Lower Sonoran Zone, *Prosopis juliflora* (Swartz) DC. and *Larrea tridentata* (DC.) Coville.

The surface vegetation between this crossing and the northern tip consists mainly of a variety of scattering grasses and shrubby xerophytes. The large or woody species listed below are the most prominent on the northern half of the length of the lava, which without question lies in the Upper Sonoran Zone.

**Artemisia dracunculus* var. *glauca* (Pallas) Harv. and Gray (f)
**A. filifolia* Torr. (f)
**A. ludoviciana* Nutt. (prairie sage) (o)
Atriplex canescens (Pursh) Nutt. (four-wing saltbush) (f)
**Baccharis ramulosa* A. Gray (yerba de pasmo) (o)
**Berberis haematocarpa* Wooton (red hollygrape) (o)
**Brickellia californica* (Torr. and Gray) Gray (o)
**Celtis reticulata* Torr. (hackberry) (f)
**Cercocarpus breviflorus* A. Gray (mountain mahogany) (o)
**Dalea formosa* Torr. (feather peabush) (f)
**Dasylirion wheeleri* S. Wats. (sotol) (f)
Ephedra torreyana S. Wats. (joint fir) (f)
Eurotia lanata (Pursh) Moq. (winterfat) (f)
Fallugia paradoxa (D. Don) Endl. (Apache plume) (f)
**Garrya wrightii* Torr. (silktassel) (o)
**Juniperus monosperma* (Engelm.) Sarg. (one-seeded juniper) (f)
Lycium pallidum Miers (f)
**Nolina microcarpa* S. Wats. (beargrass) (f)
Opuntia engelmannii Salm.-Dyck (f)
O. imbricata Engelm. (cholla, cane cactus) (f)
**O. leptocaulis* DC. (rattail cactus) (o)
**Rhus trilobata* Nutt. ex Torr. & Gray (skunkbush) (f)
Senecio longilobus Benth. (woolly groundsel) (o)
Yucca baccata Torr. (f)

* Species marked by an asterisk in this list and those which follow were not found growing on the plain surrounding the lava.

Three large semi-succulents, *Dasylirion* (Fig. 4), *Nolina* and *Yucca,* and the succulent Opuntias, prominent within the lava flow, occur as post climaxes on escarpments, talus slopes, and rocky hills from western Texas to Mexico and eastern California. *Opuntia engelmannii* and *O. imbricata,* early invaders of disturbed rangeland which become established through fragmentation (Anthony 1954) occur more frequently than other cacti on the surrounding plain as well as throughout much of the lava flow. The survival of cacti

FIG. 4. *Dasylirion wheeleri* (in flower), *Opuntia imbricata,* and other vegetation characteristic of lava depressions on that part of the recent flow within the Upper Sonoran Zone.

within the malpais is favored by an extensive, shallow root system with a few deep branches which penetrate the crevices, permitting absorption from several levels.

Other than a number of grasses, the following are the 6 more conspicuous herbaceous species on the northern half of the lava:

Chrysopsis hispida (Hook.) DC. (o)
**Eriogonum abertianum* Torr. (o)
**E. tenellum* Torr. (o)
**Polanisia uniglandulosa* (Cav.) DC. (f)
Sphaeralcea incana Torr. (o)
Verbena wrightii A. Gray (o)

Of the 14 species, other than grasses, which appear most conspicuously throughout the length of the volcanic deposit, *Atriplex canescenes, Fallugia paradoxa, Rhus trilobata, Polanisia uniglandulosa,* and *Senecio longilobus* are the most widely distributed.

In the vicinity of Oscuro, approximately 28 miles below the northern tip, the lava narrows down to a neck about ½ mile wide. This upper margin of the lower third of the lava flow is taken as the northern border of the Lower Sonoran Zone proper, which begins at an altitude between 4,000 and 4,500 feet in this section of the state. The species most characteristic of lava surfaces in the Lower Sonoran Zone, in addition to *Larrea tridentata, Prosopis juliflora,* and the 5 listed above as occurring throughout the volcanic deposit, are:

**Artemisia bigelovii* A. Gray
**Ephedra viridis* Coville (joint fir) (o)
**Lippia wrightii* A. Gray (o)
**Opuntia leptocaulis* DC. (rattail cactus) (o)
Salvia henryi A. Gray (o)

Vegetation of the alkaline plain and roadsides within the lava

A total of 51 species, other than grasses, were observed on the alkaline plain surrounding the lava. Of this number, 11 are among the 38 species found to grow along roadsides within the lava. Only 33 of the total number of species along such roadsides or on the marginal plain have not invaded the lava proper. The list which follows includes the more prominent of these roadside and range species.

Actinea odorata (DC.) Kuntze (bitter rubberweed) (o, plain)
Aplopappus heterophyllus A. Blake (rayless goldenrod, jimmyweed) (r, plain)
Artemisia tridentata Nutt. (big sagebrush) (o, plain)
Asclepias brachystephana Engelm. (o, roadsides)
A. capricornu Woodson (goat's horn or creeping milkweed) (o, roadsides)
Astragalus spp. (loco, milkvetch) (1, plain)
Bahia absinthifolia Benth. (4, plain)
Baileya multiradiata Harv. and Gray (desert marigold) (3, plain)
Chamaesaracha spp. (o, plain)
Cirsium ochrocentrum A. Gray (thistle) (o, plain and roadsides)
Datura stramonium L. (Jimson weed) (2, plain)
Fouquieria splendens Engelm. (ocotillo) (1, plain)
Grindelia aphanactis Rybd. (gumweed) (o, plain and roadsides)
Helianthus annuus L. (o, plain and roadsides)
H. ciliaris DC. (o, plain and roadsides)
Iva dealbata A. Gray (marsh elder) (2, roadsides)
Lepidium alyssoides A. Gray (peppergrass) (o, plain and roadsides)
Opuntia clavata Engelm. (o, plain)
Parthenium incanum H.B.K. (r, plain)
Perezia nana A. Gray (o, plain and roadsides)
Salsola pestifer A. Nels. (Russian thistle) (o, plain and roadsides)
Sida lepidota A. Gray (o, roadsides)
Solanum eleagnifolium Cav. (o, plain and roadsides)
Sphaeralcea spp. (two) (o, roadsides)
Yucca elata Engelm. (palmilla) (f, plain)
Verbesina encelioides (Cav.) Benth. and Hook. (crownbeard) (o, plain and roadsides)
Zinnia grandiflora Nutt. (zinnia) (o, plain and roadsides)

While 33 species growing on the grazed surrounding plain or along the roadsides within the lava have not invaded the lava proper, the malpais vegetation is much more diversified as to total species, numbering 114, exclusive of grasses, and in that a vareity of vegetation can be seen in surface pockets in any direction. Especially the crevices of the northern extension support a greater diversity and a more mesic type of vegetation than the adjacent non-lava plain.

Yucca baccata, a species with a thickened leaf and leaf base adapted for storage purposes, is typical particularly of that part of the lava within the Upper Sonoran Zone. It is found only sporadically in the surrounding area, mainly on the east side of the lava toward the northern tip. In places along the west margin of the recent flow, opposite the crater, *Yucca elata* occurs in stands (Fig. 5), but only two much-dwarfed plants were observed within the lava, apparently because this species prefers a decidedly alkaline soil, and the poorly branched main roots tend to run laterally for 5 to 10 feet. A growth of *Yucca elata* is assumed to indicate a soil rich in lime. While two trees of

FIG. 5. While *Yucca elata* occurs in stands marginal to the lava, only two plants were observed within the malpais.

Juglans major (Torr.) Heller occur along the half mile of the Oscuro road which passes through the lava, none are found within 40 miles in the surrounding country. Nor does *Celtis reticulata,* characteristic of the northern half of the lava, occur outside the malpais in this part of the state.

FIG. 6. Lava boulders thrown on the alkaline plain at the southernmost tip of the flow.

Soil moisture appears to be the most important single factor in determining the distribution of these two tree species.

The lava terminates about 15 miles north of the Alamogordo gypsum deposit in a narrow tip where the last energy of the extrusion scattered the plain with basalt boulders (Fig. 6). Flood waters discharged from the surrounding mountains deposit alkaline salts which accumulate in this and similar low areas. A distinct zonation in vegetation results from the increasing alkalinity toward the center of the basin. This zonation is reflected where on either side of the southern extension of the lava the alkaline plain supports only scattering grasses and occasional specimens of *Prosopis juliflora, Atriplex canescens, Aplopappus heterophyllus, Larrea tridentata,* rarely a much-dwarfed *Yucca elata* and *Allenrolfea occidentalis* (S. Wats.) Kuntze. *Allenrolfea occidentalis* is generally accepted as an indicator of saline soils incapable of crop production, while *L. tridentata* is characteristic of broken, rocky soil with little value for grazing. Along the west margin of the lava, *Baileya multiradiata, Fouquieria splendens, Opuntia engelmanii,* and *O. imbricata* in the marginal plain are found no nearer the southern tip than a point 15 miles to the north.

Along the margin of the lava about 1½ miles to the northwest of the lower tip, Malpais Spring escapes from a crevice, forming a pool (Fig. 7) which is elliptical in outline and measures about 50 by 80 feet at its widest and longest points. Issuing from the lava at the estimated rate of several second-feet, the water is so highly mineralized as to be unfit for human consumption or for grazing animals.

Water escapes from the pool by three divergent streams, two of which in late August were completely absorbed into the soil within a short distance, but one of which was spread to a depth of several inches for a distance of approximately a mile over a marshy area about a hundred yards wide. There is no outflow at the lower end of the flooded land, the water disappearing into the earth, which is characteristic for the loose gravels of the Tularosa Basin. Soil marginal to the overflow from the pool is white encrusted with gypsum. *Distichlis stricta* (Torr.) Rydb., *Typha latifolia* L., *Clappia suaedifolia* A. Gray, and *Scirpus americanus* Pers. grow abundantly around both the pool and the overflow. *Sorghum halepense* (L.) Pers. grows sporadically in the nearby fallow land.

Crevice and sink-hole vegetation

The 3 fern species, *Cheilanthes feei, Notholaena standleyi,* and *Pellaea longimucronata,* along with *Senecio quaerens* Greene and *Clematis ligusticifolia,* grow exclusively in sink-holes or deep crevices, usually appearing from wall niches rather than at

FIG. 7. Elliptical pool formed around Malpais Spring which issues from margin of lava.

the bottom of the depression subject to flooding during even light rains. Many other herbaceous species, particularly the grasses and *Eriogonum* spp., sometimes grow in crevices and sink-holes, usually on the dirt-filled floor, but occur more frequently as a less luxuriant growth in shallow pockets of earth on the lava surfaces. *Rhus trilobata* and *Brickellia californica* are shrubs characteristic of lava surfaces, particularly in the northern half of the flow, which sometimes also grow from crevices.

Crater and cinder cone vegetation

About 2½ miles from the northern tip of the younger flow, a steep, cinder-covered cone approximately 100 feet high stands at the apex of a flat cone about a mile in total diameter (Meinzer and Hare 1915). The unimpressive crater, which is about 150 feet across and 25 feet deep, is filled with loose, porous cinders up to 1 cm. wide (Fig. 8), and at present contains no true volcanic ash. Nitrogen is not a limiting factor to plant growth in this substrate as it is in fresh volcanic ash. The micro-Kjeldahl leaf nitrogen of the species growing within the crater, ranging from 3.49 to 4.14 per cent of the dry weight, and the total nitrite and nitrate of the crater soil samples, averaging 5 p.p.m., compare favorably with those collected elsewhere in the volcanic deposit and the surrounding area. The 12 plant species forming a sparse growth within the crater in late June are invaders from the surrounding lava.

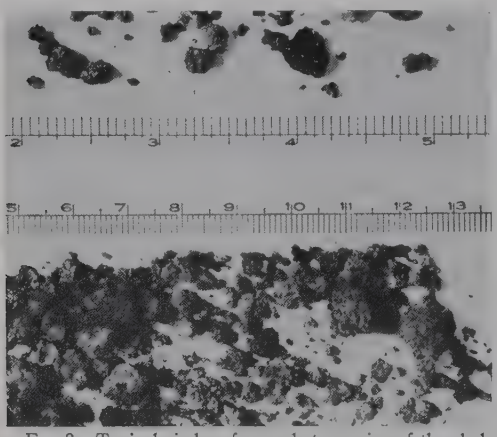

FIG. 8. Typical cinders from what remains of the shallow recent crater.

Kipouka vegetation

The one observed *kipouka* (Fig. 9), a small island covering several acres approximately 10 miles south of the crater, supports a more abundant growth of the same vegetation as on the surrounding lava plus 3 additional species, *Populus wislizenii* (Wats.) Sarg., *Tamarix gallica* L., and *Marrubium vulgare* L. The several *P. wislizenii* trees on this island grow near a shallow well, but this species is not found elsewhere within the lava flow nor in the immediately surrounding plain. *Tamarix gallica* was observed only at this site in that part of the laval flow within the Upper Sonoran Zone, but in the sapling stage appears occasionally above Malpais Spring. It is said locally that these two tree species were not deliberate introductions to the island, but seeded in. *Tamarix gallica* within the malpais, however, like that growing elsewhere in the southwest, represents an original escape from cultivation, this species having been introduced from Spain by the early priests in the area rather than occurring indigenously as its abundance and wide distribution would suggest. The only stand of *Marrubium vulgare* L. was on this *kipouka* at the site of an old goat corral, but the plant was observed once along a roadside within the lava flow. According to Wooton and Standley (1915), this species is usually to be found in places where sheep or goats have been kept.

Malpais vegetation compared to that of the Alamogordo gypsum sand and of the McCarty's lava flow

The Alamogordo gypsum deposit, approximately 224 square miles of drifting calcium sulfate (97%), and the lava flow are separated by only 15 miles. These two areas, however, have in common only the following 20 species, 5 of which are grasses and 6 others of which occur within the lava only along roadsides:

Atriplex canescens (Pursh) Nutt. (fourwing saltbush)
Cucurbita foetidissima H.B.K. (wild gourd)
Ephedra torreyana S. Wats. (joint fir)
Gutierrezia sarothrae (Pursh) Britt. & Rusby (snakeweed)
Aplopappus spinulosus (Pursh) DC. (roadside)
Helianthus annuus L. (annual sunflower) (roadside)
Lepidium alyssoides A. Gray (peppergrass) (roadside)
Lycium berlandieri var. *parviflorum* (Gray) Terrac.
Populus wislizeni (Wats.) Sarg.
Rhus trilobata Nutt. ex Torr. & Gray (skunkbush)
Salsola pestifer A. Nels. (Russian thistle) (roadside)
Sphaeralcea angustifolia (Cav.) G. Don
S. incana Torr.

Verbesina encelioides (Cav.) Benth & Hook. (crownbeard) (roadside)
Zinnia grandiflora Nutt. (zinnia) (roadside)
Andropogon scoparius Michx. (little bluestem)
Muhlenbergia pungens Thurb. (sandhill muhly)
Oryzopsis hymenoides (Roem. & Schult.) Ricker
Sporobolus airoides Torr. (bunchgrass)
S. cryptandrus (Torr.) A. Gray (sand dropseed)

The approximately 70 plant species growing mainly in the peripheral dunes and flats of the gypsum deposit represent a large fraction of the vegetative climax on the adjacent desert plain, subjected subsequently to the selective action of drifting gypsum, high light intensity and a pronounced nitrogen deficiency. A dune tolerance which involves one or more of the several possible adjustments to moving sand is important in the survival of vegetation in this substrate. Four species conspicuous in the gypsum deposit are absent from or occur sparsely on the adjacent plain:

Abronia angustifolia Greene (sand verbena)
Comandra pallida A. DC. (bastard toadflax)
Populus wislizeni (Wats.) Sarg. (cottonwood)
Rhus trilobata Nutt. ex Torr. & Gray (skunkbush)

Two of these species, *P. wislizenii* and *R. trilobata,* are found within the lava.

Five species common in the Alamogordo white sands are gypsum indicators which do not occur in the surrounding plain, are not commonly found in quartz sand deposits and, with the exception of *Frankenia jamesii,* do not occur within the lava:

Andropus carnosus (Wooton) Brand
Bouteloua breviseta Vasey
Frankenia jamesii Torr.
Greggia camporum linearifolia Jones
Selinocarpus chenopodioides A. Gray

While *Prosopis glandulosa* serves as a nucleus for quartz sand dune formation in southern New Mexico, and grows where gypsum spills over the desert plain adjacent to the white sands, it does not survive in even the younger dunes or intervening flats of the gypsum deposit. *Larrea tridentata* is conspicuously absent from the gypsum and from the marginal plains, apparently because

FIG. 9. ***Populus wislizenii*** and ***Tamarix gallica*** grow beside a shallow well on an island (*kipouka*) left within lava.

of the excessive salt content of this part of the Tularosa Basin. Only two species, *Oryzopsis hymenoides* and *Abronia angustifolia,* survive within the older interdunal depressions. *Abronia angustifolia* does not grow within the lava, and *Oryzopsis hymenoides* occurs infrequently. While the halophytes *A. angustifolia, Atriplex canescens, Distichlis spicata* (L.) Greene, and *Sporobolus airoides* Torr. grow within the gypsum deposit, the non-succulent *Eurotia lanata* and the succulent *Allenrolfea occidentalis,* halophytes which have seeded into the lava flow, are apparently not sufficiently dune-tolerant to survive the drifting gypsum.

Lindsey (1951) listed the 76 species of vascular plants most characteristic of the McCarty's lava flow at Grants, New Mexico. The 18 of these species which are also found within the Carrizozo lava flow occur throughout the state at elevations between 4,000 and 7,000 feet and are not especially characteristic of lava habitats. The Carrizozo flow differs from McCarty's flow in the barrenness associated with the recency of outpouring, in lying at an elevation lower by several thousand feet, and in the absence of high pinnacles, water-filled sink-holes, and ice caves.

There are no plant indicators of lava as there are indicators of gypsum though a number of species within the Carrizozo malpais do not tolerate the greater aridity of the surrounding alkaline plain. Also, the volcanic deposit represents a habitat which has not recently been disturbed, being protected by the ruggedness of the terrain for most of its length from invasion by domestic grazing animals though deer, rabbits and a number of smaller forms feed off the vegetation. The flora of the lava represents those species which had the opportunity to seed in and were favored subsequently by the particular combinations of climatic conditions and sheltered habitat provided by the lava surfaces but not by the included roadsides or the surrounding plain.

Summary

1. There were two reasons for observing the diversity and distribution of vacular vegetation within the Carrizozo lava flow in south-central New Mexico. (a) This is one of the youngest volcanic deposits in the United States, estimated to have been extruded within the past 1,000 years. (b) According to vegetation indicators, approximately the northern 29 miles of the 44 miles of length of this volcanic flow lie within the Upper Sonoran and the southern 15 miles extend into the Lower Sonoran Zone.

2. The Carrizozo volcanic deposit, plus the included graded roadsides and the surrounding alkaline plain, supports an observed total of 49 families, 125 genera, and 175 sepcies of vascular plants. The 37 species of Compositae and 24 of Gramineae are numerically the most abundant, and either family occupies far more area than any of the others represented. Varying from ½ to 5 miles in width, the lava bed covers approximately 120 square miles.

3. *Juniperus monosperma,* an indicator of the Upper Sonoran Zone, can be found throughout the northern two-thirds of the lava while toward the southern tip two Lower Sonoran indicators, *Larrea tridentata* and *Prosopis glandulosa,* are conspicuous. The overlap of the vegetation of the two zones can be seen within the lava approximately 10 miles below Carrizozo where there is a scattering growth of all 3 species. Of the 14 species, other than grasses, which appear most prominently throughout the length of the volcanic deposit, *Atriplex canescens, Fallugia paradoxa, Rhus trilobata, Polanisia uniglandulosa,* and *Senecio longilobus* are the most widely distributed.

4. Favored by the moist, sheltered crevices near the crater and by the 3 inches greater annual precipitation toward the northern tip of the flow, 99 species, other than grasses, characterize that half of the lava definitely within the Upper Sonoran Zone, compared to 28 species on the more xeric third in the Lower Sonoran Zone. The improved moisture conditions toward the northern extremity are associated with an increase in altitude from 4,100 feet at the southern end to 5,300 feet at the opposite tip.

5. In part as a result of the protected sink-holes and crevices which efficiently collect and retain soil and moisture, the lava proper supports a greater diversity of species, 114 exclusive of grasses, than either the surrounding plain (51 species) or the roadsides within the lava (38 species). Only 33 species found to grow along roadsides or on the range adjacent to the malpais have not invaded the lava, whereas the basalt surface supports 62 species not observed on the surrounding plain and 76 species not to be found along roadsides within the lava bed. Three ferns and 2 other species occur only in sink-holes and crevices. The 12 species within the crater are to be found on the surrounding lava. An island left in the volcanic flow supports mature trees of *Populus wislizenii* and *Tamarix gallica.*

6. Only 20 species, including 5 grasses, are common to both the Carrizozo lava bed and the Alamogordo gypsum deposit, which extends to within 15 miles of the southern tip of the lava. The volcanic deposit supports almost twice as many species as the gypsum bed of almost double

its area. The lack of similarity in the vegetation of the two peculiar environments is in part attributable to the greater protection afforded by the deeper depressions of the lava, the extreme salinity of the intervening Tularosa Basin, and the selective action of the drifting gypsum, which is 97% calcium sulfate and deficient in organic matter, nitrogen, and a number of other nutrients.

7. The 18 vascular species which are common to both the McCarty's flow at Grants, New Mexico, and the Carrizozo malpais occur throughout the state at altitudes between 4,000 and 7,000 feet. There are no specific plant indicators of lava, as there are of gypsum, but a number of plant species within the lava flow do not tolerate the greater aridity of the surrounding alkaline plain. Protected from domestic grazing animals by the ruggedness of the terrain, the volcanic deposit represents an essentially undisturbed habitat, characterized by vegetation which after seeding in was subjected to less extreme selective action of the environment than that of the roadsides or the surrounding plain.

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THE MICROBIOLOGY OF FLATHEAD AND ROGERS LAKES, MONTANA
I. PRELIMINARY SURVEY OF THE MICROBIAL POPULATIONS[1]

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Henrici (1939) and ZoBell (1946) have pointed out that although many investigations have been made of the microbiology of aquatic environments, more information is needed before the activities of these microorganisms are understood. In 1951, a study of two lakes in Montana was initiated to gain more information on this subject. This report covers the preliminary survey made that year. In carrying out investigations on the role of microorganisms in lake water a prime requisite is a relatively undisturbed area, one in which there has been comparatively little interference with the typical ecological situation. The two lakes chosen fitted this requirement (Graham and Young 1934, Young 1935, and Brunson and Nelson 1952). The survey of Graham and Young (1934) on the bacteriology of Flathead Lake provided a point of departure for these studies.

It is a pleasure to acknowledge the cooperation of the Biological Station of Montana State University and particularly that of Dr. Royal Bruce Brunson who generously and graciously aided the authors in locating stations and obtaining samples.

Materials and Methods

Both Graham and Young (1934) and Young (1935) have described Flathead Lake as an oligotrophic lake. It is approximately 35 miles long with an average width of 7 miles and a maximum depth of some 100 meters. Since the publication

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of these papers, Kerr Dam has been completed and as a result the level of the lake has been raised about 10 feet. Because of limited information, the exact locations of the sampling points used by Graham and Young could not be duplicated. The stations selected for study represented four distinct localities: the inlet area (Flathead Delta, FD), the outlet area (Polson Bay, PB), the deep area (Yellow Bay, deep, YB-D), and a protected bay (Big Arm Bay, BA). These four sites corresponded approximately to stations number 4, 2, 1, and 10 of Graham and Young. Their locations are shown on the map of Flathead Lake published by Graham and Young (1934). For Rogers Lake, the areas used were the inlet (RL-1) and the open lake (RL-3). A map of Rogers Lake appears in the paper of Bunson and Nelson (1952).

Two collections were made at all stations in the period from June 25 to July 17, 1951, in order to determine consistency of population over a short period of time and to avoid undue emphasis of temporary or shifting environmental conditions. Temperature and pH of each sample were determined immediately after collections. pH was determined colorimetrically. Because of limited facilities at the time of this preliminary survey, water samples were collected in a one liter Kemmerer water sampler which was disinfected with "Roccal." Since Graham and Young (1934) had found the maximum population at approximately 5 feet, the depth of sampling was set arbitrarily at 5½ feet. Bottom mud samples were secured by means of a "Roccal" disinfected Ekman dredge. Soil samples were collected in sterile containers by means of disinfected or sterilized implements.

As soon as possible after returning to the laboratory, the samples were diluted and plated in triplicate with sodium caseinate agar (Fred and Waksman 1928). It is recognized that the use of any single medium imposes limits, but long years of experience have provided evidence that this particular nutrient agar gives optimum and reproducible results for the isolation and enumeration of bacteria, actinomycetes, and fungi when compared with other media commonly used for this purpose. Qualitative test solutions (Fred and Waksman 1928) for determining the presence of denitrifiers, urea decomposing microorganisms, nitrifiers, and *Azotobacter* were inoculated. All plates were incubated for 3 weeks at room temperature. This extended period allowed for full development of the slow growing colonies, especially the fungi. Qualitative tests were incubated from 3 to 7 weeks.

Results

Little difference in temperature or pH was noted between the two collections at each station. Temperatures recorded for water samples ranged from 11-20° C; for mud, 5-20° C; and for soil, 13-20° C. The deeper the station, the lower the temperature was for the mud samples. Most samples were slightly alkaline in reaction but total ranges showed 7.6-8.2 for water; 6.8-7.8 for mud; and 6.6-8.0 for soil.

Nitrifying organisms were usually present in soil and mud samples, particularly nitrosofying organisms. Rogers Lake samples from the bottom of the open area (RL-3) contained no nitrifiers. However, this bottom sample was not a typical mud sample, but rather a dark green gelatinous mass resembling partially decomposed organic matter. A limnological survey in 1950 (Brunson and Nelson 1952) showed a high population of blue-green algae which might account for this type of bottom. The only water sample which contained nitrifying organisms was the second sample from Polson Bay. All samples contained denitrifiers but evidently there were few organisms present which are capable of producing free nitrogen. None of these was found in the soil samples. Nitrite was the most common product of the denitrifiers. Many urea decomposers were found in each sample. Microscopic examination of mannitol enrichment cultures revealed *Azotobacter* from all samples.

All quantitative results are given in Table I. The largest numbers of bacteria in the water samples from Flathead Lake were found in those samples from the inlet area, Flathead Delta (FD), and the outlet area, Polson Bay (PB). Counts from the shallow station of Rogers Lake (RL-1), were of comparable magnitude but this sample was from a depth of 0.3 meter whereas all other water samples were taken at the 5½ foot level. The lowest counts occurred in the samples from Big Arm Bay (BA) and Rogers Lake, RL-3, the open area. Generally, the counts were higher in the first set of samples than in the second set. A notable exception to this was the second sample from Polson Bay. At that time there was a decided *Anabaena* bloom in the water. Henrici (1937) has shown that an increase in plankton is accompanied by an increase in bacterial population.

When the mud samples are ranked according to the numbers of bacteria present, the order is the same as that obtained in ranking the water samples. The numbers present in the Rogers Lake sample from the open area (RL-3) were very low. The organic nature of the bottom there indicates that bacteria are not actively decomposing the deposited materials. In turn, the small bacterial population suggests that the number present may

TABLE I. Microbial populations of water, mud, and soil from Flathead and Rogers Lakes, Montana, 1951

Sample	Depth	Station	Date	Bacteria	Per cent Chromogens	Fungi	Actinomycetes
				X10²		X10	X10
Water	5½ ft.	YB-D	6-25	2.30	21	40.0	15.0
per ml		YB-D	7-13	2.14	54	16.0	0.0
		PB	6-25	27.0	25	40.0	15.0
		PB	7-17	258.0	44	0.5	0.1
		FD	7-1	72.0	48	1.0	0.1
		FD	7-15	10.4	60	0.4	0.1
		BA	7-1	0.66	61	2.5	0.0
		BA	7-13	0.61	51	2.0	0.0
		RL-1	7-3	52.0	38	0.2	0.1
		RL-1	7-11	26.5	35	1.0	0.0
		RL-3	7-3	0.63	39	0.1	0.0
		RL-3	7-11	0.44	36	0.0	0.0
				X10⁶		X10³	X10³
Mud	77.0 m	YB-D	6-25	2.76	4	40.0	50.0
per gm		YB-D	7-13	2.60	42	10.0	10.0
	2.0 m	PB	6-25	89.8	34	450.0	1,100.0
		PB	7-17	20.5	79	3.0	300.0
	8.0 m	FD	7-1	121.0	54	2.0	2.0
		FD	7-15	44.0	61	5.0	4.0
	17.0 m	BA	7-1	1.56	49	4.0	0.0
		BA	7-13	1.56	49	3.0	25.0
	0.3 m	RL-1	7-3	104.0	53	2.0	11.0
		RL-1	7-11	81.6	58	6.6	10.0
	5.7 m	RL-3	7-3	0.0215	60	5.0	0.0
		RL-3	7-11	0.095	54	0.02	0.02
				X10⁶		X10³	X10³
Soil		YB-D	6-27	42.0	9	350.0	1,800.0
per gm		YB-D	7-10	290.0	29	50.0	270.0
		PB	6-27	126.0	27	10.0	130.0
		PB	7-10	134.0	30	66.0	130.0
		FD	7-1	31.5	17	40.0	30.0
		FD	7-15	31.0	48	50.0	80.0

be one of the limiting factors in decomposition. With the exception of Rogers Lake, RL-3, and Big Arm Bay, the first counts exceeded those of the second sampling.

The percentage of chromogens in the water varied greatly. In the samples from Flathead Lake, the figure was usually higher for the second sample; it was lower for the second sample taken at Rogers Lake, for both RL-1 and RL-3. The highest proportion of chromogens found was in the samples from Big Arm Bay which also had the smallest bacterial population. In bottom samples, the percentage of chromogens was higher in the second set of samples with one exception, Rogers Lake, RL-3. The proportion of chromogens in bottom mud samples exceeded that from the water samples except for the Yellow Bay and Big Arm samples.

Actinomycetes and fungi were present in most samples, but the numbers representing these groups in the water were very low. As a result, no value can be placed on the absolute numbers although the figures indicate their relative paucity. Both groups were present in most bottom samples and in all soil samples. The common order of population gradient for the actinomycetes and fungi isolated from all three types of samples taken at Yellow Bay, Flathead Delta, and Polson Bay was from water to bottom mud to soil in increasing order.

Although quantitative results for fungi are inconclusive some of the particular isolates were interesting. These included *Sporobolomyces salmonicolor* from the Yellow Bay mud, a sterile basidiomycete with clamp connections, *Candida albicans* and other representatives of imperfect fungi. Forms commonly encountered in water and soil isolations, such as species of *Aspergillus, Penicillium,* and representatives of the *Mucorales* and *Saprolegniales* were strikingly rare in occurrence or not found at all. The species from the soil samples were found freely in the mud suggesting surface washing. This was especially noticeable at Flathead Delta, the inlet area.

Many of the plates from mud samples contained large numbers of algal colonies. Samples from Rogers Lake often had more colonies of algae than other microorganisms. Several species of *Scenedesmus,* representatives of *Chlorella, Chlamydomonas, Chlorococcum* and *Ankistrodesmus* were isolated in large numbers. Henrici and McCoy (1938) found large numbers of algae in bottom deposits of oligotrophic lakes.

Three soil samples from areas adjacent to the sampling stations in the lake were examined. For Yellow Bay, a soil sample was taken from the bank of a stream flowing into Flathead Lake. The soil of the first sample was wet but by the time of the second sampling it was dry. The Polson Bay soil sample represents silt which has filled in a portion of that region. The sample was taken a few hundred yards from open water; it was waterlogged. At Flathead Delta, the sample was obtained from water-logged soil in an area which is submerged during high water. A large part of the delta area, originally dry land, is now permanently under water as a result of the installation of Kerr Dam. As a consequence, the area is marked by a heavy stand of dead trees, many of which are washing into the open lake now.

The second Yellow Bay soil sample contained the largest bacterial population and the Flathead Delta samples the smallest. The second samples from both Yellow Bay and Polson Bay yielded increased numbers of bacteria besides showing an increase in the percentage of chromogens present. The proportion of chromogens in the second set of samples was of the same magnitude as that of the water samples, but generally lower than that of the mud samples. All three soil samples contained

significant numbers of actinomycetes and fungi. In general, the numbers representing these microorganisms were higher than those from comparable mud samples.

Total microbial population figures showed a numerical spread from the lowest counts in water to highest counts in soil, with the notable exception of Flathead Delta where the numbers found in both mud samples exceeded those from the soil.

Discussion

Results of this investigation of Flathead Lake and the earlier one by Graham and Young (1934) show some similarities but also differences. Only bacterial populations of the water can be compared directly since Graham and Young did not consider other microorganisms or the populations of associated bottom samples in their studies. The general absences of nitrifiers in the water samples and the presence of denitrifiers capable of producing ammonia and nitrite but seldom free nitrogen, is in general agreement with the results reported by Graham and Young. The 1951 bacterial counts for water samples were higher than those obtained by the earlier investigators, with the exception of the Big Arm Bay counts. Graham and Young showed however, that the numbers of bacteria present in the water at one given station varied considerably during the year. The two samples from each station in 1951 gave results indicating that the size of the population was consistent during the period of investigation, unless there was a conspicuous change in some environmental factor. Such an unusual change was the algal bloom observed in Polson Bay at the time of the second sampling and reflected in the bacterial counts of that sample.

Flathead Lake is a large oligotrophic lake and Rogers Lake a small eutrophic lake. Yet the variations in the numbers of microorganisms from different areas of the lakes seemed to be more significant than the variations ascribable to the type of lake. With both water and mud samples, it was found that the inlet areas of both lakes had higher populations than most of the other locations. Shallow protected bays of the Polson Bay type, had large numbers of microorganisms, a condition previously noted by Henrici and McCoy (1938). Large, deep protected bays reputedly have populations of the order of open lakes. Certainly Big Arm Bay, an example of such a bay, is itself larger than many lakes.

The percentage of chromogens in water samples was higher than that reported by Graham and Young. The general increase in the percentage of these organisms in the second set of samples indicates a change in the qualtitative nature of the environment, for the total number of microorganisms in the water remained fairly consistent. Fred, Wilson, and Davenport (1924) and Graham and Young (1934) have demonstrated that microbial populations in water fluctuate greatly over a significant period of time. Such fluctuation was observed here in the changing chromogen population.

The numbers of fungi and actinomycetes in water are small. Counts from water, mud, and soil samples in comparable areas show an increasing population gradient in that order. This is in general agreement with known observations on populations from such habitats. The fact that a few fungi and actinomycetes have been found repeatedly may indicate that these represent species which are able to exist, at least temporarily, in a dilute nutrient environment.

Numbers of microorganisms in the soils sampled were moderately high. The water-logged soils of Polson Bay and Flathead Delta, had a higher percentage of chromogens, of the order found in water samples. These soils also had smaller numbers of fungi and actinomycetes than the well drained Yellow Bay soil. Actually, the samples from Polson Bay and Flathead Delta had biological and physical characteristics closely resembling the muds of these areas. As yet too little information is available about the factors influencing microbial populations in aquatic environments to make any meaningful comparisons (Henrici 1939).

Summary

A preliminary survey of the microbial populations of Flathead Lake, a large oligotrophic lake, and Rogers Lake, a small eutrophic lake, was made during the summer of 1951. The microbial population present in three types of samples studied from Yellow Bay, Polson Bay, and Flathead Delta, tends to show a decided increase in numbers from water to mud to soil. Variations in numbers recorded from different areas of a lake suggest that the area of the lake is more significant than the type of lake according to limnological classification. It appears that the inlet areas of both lakes have higher microbial populations than most of the other areas sampled.

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DIFFERENTIAL RESPONSES TO CLIPPING OF SIX PRAIRIE GRASSES IN WISCONSIN[1]

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Certain of the native grasses of the tall grass prairie either have disappeared from or have been greatly weakened in grazed areas where they were abundant at the time of the advent of the white man and his domestic animals. That the rapid demise of such prairie species as the Andropogons is directly related to grazing has been shown in many studies; relative changes in the botanical composition of grazed prairie vegetation have been related to the intensity of utilization by the grazing animal. Work by Smith (1940), Weaver and Hansen (1941), and Voight and Weaver (1951) indicates that the "decreasers" (Dyksterhuis 1949) are big bluestem (*Andropogon gerardi* Vitman), little bluestem (*A. scoparius* Michx.), switchgrass (*Panicum virgatum* L.), Canada wildrye (*Elymus canadensis* L.), and Indiangrass (*Sorghastrum nutans* (L.) Nash), while side-oats grama (*Bouteloua curtipendula* (Michx.) Torr. is classed as in "increaser."

In studies of establishment and survival of the above six species in Wisconsin (Robocker and Miller 1955), it was found that the changes in botanical composition resulting from clipping of mixed stands were in agreement with those reported by other investigators. Side-oats grama increased in density under 4 clippings made at 28 day intervals during each of the summers of 1950 and 1951; Canada wildrye increased under single midsummer clipping; big bluestem and switchgrass sharply decreased in direct relation to an increase in clipping severity. Indiangrass and little bluestem were less affected by the clipping treatments than were the other species, showing only slight changes from the controls under either system of clipping.

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The present study sought to determine some of the underlying autecological factors in these differential responses to clipping and grazing. It seemed logical to assume that in a mixed stand of these grasses, any defoliation level which removed photosynthetic tissue from the low-growing side-oats grama would remove inordinate amounts of foliage from the tall grasses, with resultant excessive reduction of photosynthesis and depletion of stored foods. This is in accordance with the often observed superiority of prostrate forms over plants of more erect growth habit with respect to persistence under severe grazing. It, however, would not suffice to explain the varying responses of plants of the same general growth form. This latter might be related to preferential grazing in pasture areas, but this could scarcely be a causal factor in clipping experiments.

Deep appreciation is expressed to Professor H. A. Ahlgren, for his valued aid and advice in the course of the study.

Methods

The investigations were carried out during 1953 and 1954, using seeded plots which had been established in 1949 during the earlier investigation at the University of Wisconsin Arboretum and at the University West Hill Farm, both at Madison. The Arboretum plots were on a low-lying, mesic, relatively fertile soil of the Celina series, while the Hill Farm plots were on a hill-top site of xeric, eroded, low-fertility soil of the Miami series. All of the plots were burned early in the 1953 season.

Life history studies

Three pure plots of each of the various species had been established on the West Hill Farm in 1949. For detailed investigation of the morphology and seasonal development of each species, one bunch was collected from each of the three plots at approximately weekly intervals from the onset

of growth until late in the season, at which time collection was made at biweekly intervals. Digging was so carried out that lateral extensions and approximately 6 inches of vertical roots were obtained with each bunch.

The plants were taken into the laboratory and examined; morphological characteristics were sketched by the senior author, and any growth changes which had occurred since the preceding collection were noted and diagrammed. Measurements included: (1) vertical height of the tallest shoots of each bunch; (2) height to the collar of each exserted leaf; (3) vertical height of stem tip; and (4) length of the longest rhizome of current season's growth. The relative ages of individuals of the various orders of aerial shoots were determined by their heights, the number of visible leaves and the number of leaves with exserted blades. Examination revealed that new growth on both roots and rhizomes was clearly distinguishable from more mature structures, by the shiny white or creamy white appearance of the external surfaces of the former. Determination of the relative maturity of lateral rhizomes was based on the length of the stem and the number of modified leaves present, and that of the roots by both length and the degree of lateral branching.

In addition to the laboratory observations, phenological records were kept for the plants at both the Hill Farm and the Arboretum.

Clipping experiments

For the 1949-1952 investigation, the seeded areas in both fields had been subdivided into 48 plots, each 10 x 40 feet. Sixteen plots had been designated as controls, 16 had been clipped 4 times annually, and 16 clipped once each season. These treatments had to a large extent purified the different plots for certain species or growth forms and these were used as semi-pure plots in the 1953 study. The original plan was to impose treatments on big bluestem and Indiangrass in the control plots of the preceding experiment, on side-oats grama in the plots clipped 4 times annually, and on little bluestem and Canada wildrye in the plots clipped once each year. It soon became obvious that Canada wildrye, which had been vigorous during the seasons of 1950 and 1951, but had not increased during 1952, was dying out in all plots. Clipping treatments of this species were discontinued and further observations concerned changes related to this decline.

The 48 plots of the earlier work were grouped into 8 blocks, each containing 2 replicates of each of the 3 different semi-pure plots. The 1953 clipping treatments were so arranged that each 10 x 40 foot plot of the various species was subdivided into 3 sections, 2 receiving clipping treatments and one used as a control.

1. Arboretum

One block of 6 plots was uncut until August 5th at which time it was clipped at a height of 3 inches to simulate cutting for hay. On May 15th, the sections to be mowed in each of the 7 remaining blocks were cut with a Jari mower. One-third of each 10 by 40 foot plot was clipped at a height between 1½ and 2 inches from the ground ("low level") and another one-third clipped at a height between 3½ and 4 inches ("high level"). Clipping was repeated at 20-day intervals throughout the season, the last (seventh) mowing being made on September 15th.

2. Hill Farm

The working hypothesis of the West Hill Farm experiment was that reversal of the differential losses of photosynthetic tissue might, to a certain extent, reverse the relative positions of big bluestem and side-oats grama with respect to their responses to clipping during the original investigation.

Basal area measurements of 30 randomly selected plants of each species were made early in the season, and plants of the median basal area were used for all weight sampling.

Clipping was begun on May 20th. Prior to mowing, the photosynthetic material (that is, green leaves exclusive of dark external sheath bases) of 30 bunches of each species was removed and weighed in the field. One-third of each plot was then mowed at approximately 1½ inches from the ground. The weights of photosynthetic material still remaining on 30 bunches of each species were determined as rapidly as possible. The average weight of photosynthetic tissue per bunch removed by this cutting height, expressed as a percentage of the average pre-cutting weight per bunch was determined for each species. Side-oats grama was found to have lost approximately 35 per cent, big bluestem and Indiangrass approximately 75 per cent and little bluestem approximately 50 per cent of their respective weights of top-growth at this clipping level, and these "percentage removals" were retained for subsequent cutting treatments on this one-third of the plots. The second clipping treatment was so designed that big bluestem, Indiangrass and little bluestem lost 35 per cent and side-oats grama 75 per cent of their respective herbage weights with each defoliation. Based on the original weight of uncut plants, the weight per bunch which would result in a specific percentage removal was calculated for each species.

On May 30th, the leaves from 2 bunches of each species in the unclipped sections were clipped and weighed; using hand shears, small increments were cut from the herbage of each plant and it was reweighed until the correct weight for a specific percentage removal was obtained. The average height of the remaining leaves from the 2 sample bunches plus the height of the crowns from which the samples had been taken was used as the clipping height. Grass shears were fitted with a support, the height of which could be adjusted as desired, and used to clip all bunches of each species at the correct height to remove the desired percentage of topgrowth.

Thus, each species was subjected to 2 clipping treatments: big bluestem, Indiangrass and side-oats grama were clipped at heights removing approximately 35 per cent and 75 per cent, and little bluestem at heights removing 35 and 50 per cent of the photosynthetic tissue as determined by weighing.

After the first clipping, each species under both clipping levels was cut again when the average weight of photosynthetic material of 2 bunches was equal to the original weight, irrespective of the condition of the other species. When any species under either clipping level failed to recover the original weight within a period of 3 weeks, clipping of that particular species-treatment combination was discontinued for the season. Wherever present, elongating stems were removed from the herbage prior to weighing.

3. Analysis of clipping—both areas

1953

It was desired to count the number of shoots per bunch for each species under each clipping treatment. To ascertain the variability within each species, shoots were counted and basal area measured on 30 bunches of each species in the control plots. The values were reduced to shoots per square inch of basal area and subjected to statistical analysis in groups of ten. It was considered that an adequate sample number had been obtained when the standard error equalled 10 per cent or less of the mean. From this sampling, it was concluded that with respect to big bluestem, little bluestem and side-oats grama, 10 bunches would constitute an adequate sample size, while 20 bunches of Indiangrass were required.

Using these sample sizes and selecting bunches at random, vegetative shoots, cut stems, and uncut stems were counted and basal area measurements made in plots of all species under the various treatments at both the West Hill Farm and the Arboretum. Statistical analysis was made of each 10 or 20 unit sample and those samples in which the standard error exceeded 10 per cent of the mean were omitted from further consideration.

In October, 1953, crown samples were taken at the West Hill Farm for determination of the total available carbohydrate content. Ten plants of each species were collected from both the control and the clipped plots. Each sod was trimmed and the crown area recorded; the tops were cut to approximately three-fourths of an inch above the crown and the roots to approximately one inch below the crown. All soil and plant debris were removed by washing and the plants were killed by placement in a 100°C oven for one hour. Each sample of 10 bunches was dried in a forced-air oven at 70°C for 5 days, weighed and ground to a fine powder. The analytical methods employed were a modification of Weinmann's (1947) taka-diastase digestion and acid hydrolysis technique, followed by the Schaffer-Somogyi test of reducing capacity.

1954

In June, 1954, several measurements were made on the repeatedly clipped plants on both experimental fields, and, in addition, on plants subjected to the single midsummer clipping at the Arboretum. The number of shoots, the basal area and the over-all foliage height were determined for each of 30 bunches of each species under the different treatments. The values for shoot numbers were subjected to analysis of variance and least significant differences calculated to determine possible significant variation from the number of shoots of control plants. On June 13th, the total aerial growth from 5 bunches, median basal area in size, of each species was clipped in the controls and in the treated plots. All dead leaves and culms of the preceding season's growth were removed, the clippings were dried in a forced-air oven at 70°C for 96 hours and weighed.

Results

Descriptions of the species

It seemed impossible to distinguish between "rhizomes" and "tillers" by use of any morphological characteristics, such as point of origin, since all integradations existed between forms clearly delimited by either designation. The term "rhizome" had been used here for those stems which remained subterranean sufficiently long to possess 3 or more elongated internodes underground. Rhizomes which had grown in years prior to 1953 were designated "primary" rhizomes. On side-oats grama and Indiangrass, shoots were developed upon which the stem tips remained near the

ground during one season, overwintered and were the first to begin growth the following season. Such were distinguishable from shoots arising from buds in 1953 by the lack of transitional leaves and a complete encirclement by dead sheath bases of the preceding year's growth. These older growths will be referred to as "primary shoots." Aerial shoots arising in any one season from basal buds of primary shoots, or from buds formed the preceding year on shoots which did not resume growth, are designated as "secondary" shoots. "Tertiary" shoots arise from buds of secondary shoots, etc.

Side-oats grama.—The crowns of the plants examined were composed of masses of woody tissue and a moderately close system of slender rhizomes. At full growth, the vegetative shoots (those on which the stem tips did not elongate) possessed 4 or 5 leaves with blades exserted within a distance of approximately 2 cm., and the collar of the highest leaf was at an average height of 7 cm. from the crown. The average vertical foliage height at mid-season was between 15 and 20 cm. and the mature floral stalks ranged to approximately 80 cm. The ratio of vegetative shoots to reproductive shoots was approximately 10:1, as shown in Table I, indicating production of a relatively low number of floral stems when compared with the other 3 species. A relatively large number of total stems per unit crown area was produced. Seasonal growth (Fig. 1) began moderately early in the season and was first evidenced by the production of leaves by primary shoots. One of the unique features of this grass, when compared with the others of this study, was the high production of secondary, tertiary, and higher order aerial shoots and rhizomes (Fig. 2A) throughout the season. The crowns of all plants collected were covered with a profusion of shoots in all stages of development, and although this rapid production of shoots diminished during early July at the time of floral development, it at no time ceased.

Indiangrass.—Many of the plants had a single-stemmed appearance rather than one of a bunch or a sod, due to a relatively great extension of rhizomes, and to production of few basal shoots (Fig. 2B). In the region of what was apparently the location of the seedling plant, the stem tissues,

TABLE I. Numbers of vegetative and reproductive shoots per square inch of basal area of West Hill Farm plants. Each value is the average of 30 bunches with 5% confidence limits

Species	Vegetative shoots	Reproductive shoots
Side-oats Grama	6.03±.86	.60±.12
Indiangrass	2.49±.42	.50±.10
Big Bluestem	3.44±.67	1.13±.13
Little Bluestem	6.47±.77	3.46±.53

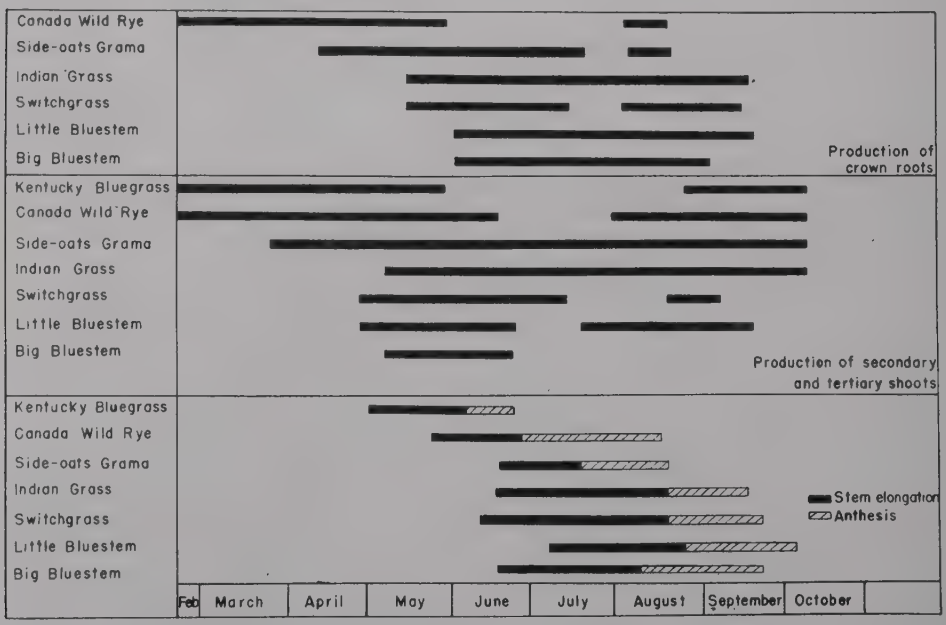

FIG. 1. Seasonal development of the prairie species. Data for Kentucky bluegrass shown for comparison.

including rhizomes and the bases of clearly aerial shoots, and the root tissues were fused into a hard woody crown mass. No quantitative data were collected on this aspect, but there seemed to be a tendency for dying out of both roots and stem tissues in the center woody mass with resultant partial fragmentation of the crown.

Mature vegetative shoots possessed 3 or 4 leaves, the exserted blades of which were clustered within an average vertical distance of 1.5 cm., at a height between 13 and 14 cm. from the shoot bases. The ultimate vertical foliage height averaged 45 cm. and the floral stalks at maturity were near 160 cm. in height. The ratio of vegetative shoots to reproductive shoots was approximately 4:1, a value considerably lower than that found for side-oats grama.

Growth began in early May (Fig. 1) with the development of leaves on some of the primary shoots, the emergence from the soil of tips of primary rhizomes and beginning development of secondary shoots. During the 1953 season, the majority of shoots which developed from basal buds turned down and grew for varying distances underground, with only a very few shoots at all times aerial. New shoot and rhizome development continued all season, but never approached the abundance to be found with side-oats grama.

Switchgrass.—No "true" crown could be described for this species, because the underground stem material consisted of a highly intermeshed system of thick rhizomes at the center, with long rhizomes extending radially to maximum distances of 1½ feet from the center (Fig. 2C). Very few basal aerial shoots were produced, most aerial growth arising from rhizome tips. The tendency for disintegration of the central regions with resultant fragmentation was pronounced. Few secondary shoots were produced directly, most aerial shoots developing from rhizomes of varying lengths or from woody "spurs"; these latter, which were found at the bases of dead stems of the preceding season, consisted of a series of short thickened nodes and internodes and were not subterranean. Primary stems were not observed. The lack of these was explicable when it was found that by the end of the season all shoots, including non-flowering shoots, had stems with elongated internodes. The flowering stems were leafy to within approximately 20 cm. of the bases of inflorescences, and possessed 6 or 7 culm leaves. The same number of leaves were found on the non-flowering elongated stems, but no floral structures were formed.

Due to the leafiness of the stems and to the elongation of all stems, the average foliage height at maturity was approximately 55-60 cm., while the average height to the tip of the inflorescence was 120 cm.

Seasonal development began in early May (Fig. 1) with the emergence of the tips of primary rhizomes from the soil and the development of these tips into leafy shoots. Development and emergence of both older rhizomes and those starting from buds continued throughout most of the season (Fig. 2C), ceasing during floral development between late July and mid-August.

Big Bluestem.—The morphology and developmental pattern of big bluestem, as found in this study, were simpler than those of the foregoing species. Of the total of 51 specimens brought into the laboratory, and the additional numbers examined in the field, all but 2 somewhat rhizomatous plants exhibited a definite bunch habit of growth and possessed high, compact and woody crown. The solid crown bases of the majority of the bunches extended as much as 4 cm. above the ground surface and were composed of fused woody masses of old stem bases and roots.

The aerial growth of the unclipped plants was composed almost entirely of secondary shoots. All of the shoots originated from buds during that season and all possessed one or, usually, two transitional leaves. Aerial shoots at the periphery of the crown grew at oblique angles from the under edge of the crown and later rooted close to their point of origin, but no internodes were developed underground (Fig. 2D). This species developed by far the most vigorous foliage of the 6 species studied. Mature vegetative shoots possessed from 6 to 8 leaves, with blades measuring between 25 and 35 cm. in length. These blades were clustered within an average vertical distance of 3 cm.; the vegetative shoots, measuring an average 15 cm. to the collar of the highest leaf, were the tallest of the 6 species. The vertical foliage height at maturity was approximately 50 cm. and floral stalks attained maximum heights near 175 cm. As shown in Table I, the ratio of vegetative shoots to reproductive shoots was approximately 3:1.

Big bluestem was the latest of these species to begin seasonal growth; however, growth was exceedingly rapid once initiated and secondary shoot development was profuse during June. By late June, dissection of several crowns indicated that very few non-growing basal buds remained, and after that time virtually no small secondary shoots were found. The axillary buds on larger shoots were well-developed and swollen in appearance (Fig. 2D), but no tertiary shoots developed from them during that season.

Little Bluestem.—The plants bore a close re-

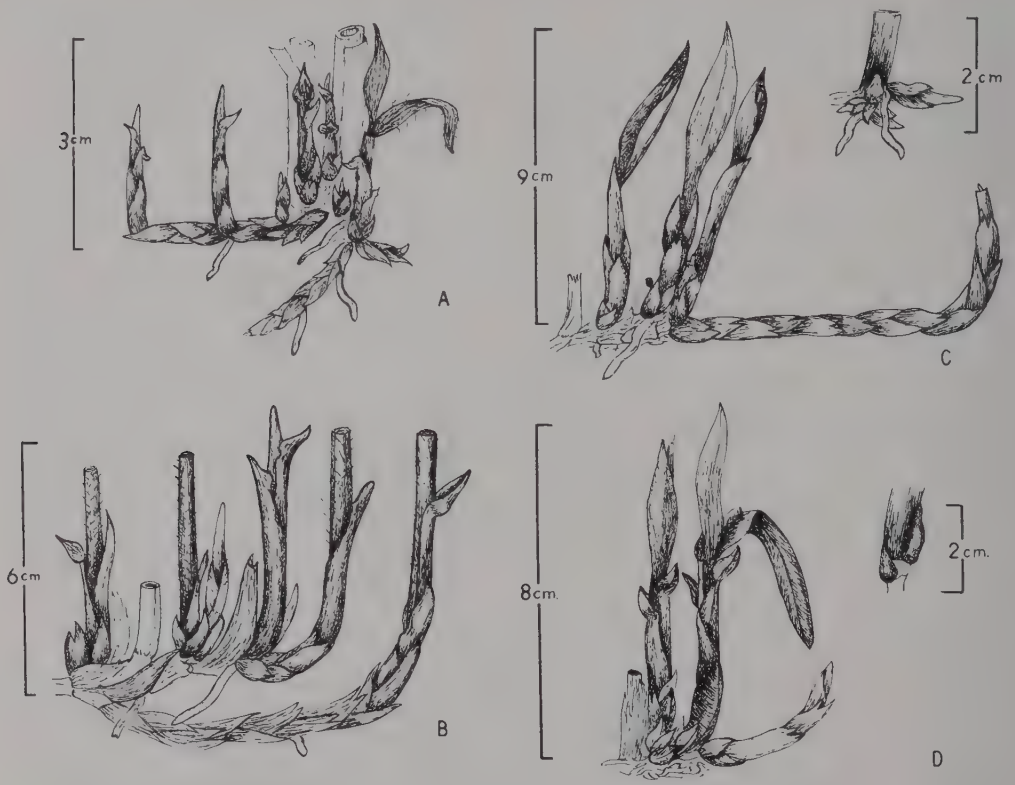

FIG. 2. Semi-diagrammatic sketches of plants showing various characteristics. A. Side-oats grama, collected May 25th, tertiary shoots at base of large secondary shoots and emergent and subterranean rhizomes; B. Indian grass, collected June 12th, base of plant; C. Switchgrass, collected June 2nd, base of plant. Inset: secondary rhizomes at base of emergent rhizome shoot; D. Big bluestem: vertical and semi-horizontal shoots, collected May 17th. Inset: lateral buds of secondary shoots on June 18th.

semblance to those of big bluestem in general morphology and possessed the same type of high, woody crown. No plants of rhizomatous habit were encountered and the peripheral shoots showed a lesser tendency than those of big bluestem to grow horizontally or obliquely from the crown. Nearly all of the aerial growth during 1953 was composed of secondary shoots, no primary shoots being found. Tertiary shoots were produced late in the season, and while they were not abundant, were in relatively higher numbers than produced by big bluestem.

The average number of shoots per unit crown area produced by this species was the highest of those studied. The ratio of vegetative shoots to floral shoots was approximately 2:1, the lowest value recorded (Table I). At maturity, the vegetative shoots possessed an average of 3 leaves, the blades of which were exserted within 2 cm. of each other on sheaths of aproximately 13 cm. in height. The vertical foliage height at maturity was approximately 35 to 40 cm. and floral stalks were near 110 cm. tall at full maturity.

Although eventually the latest of the species to flower, little bluestem gave some evidence of dormancy break as early as March 20th, when several small secondary shoots had broken through the bud scales and were pale green, although the major growth did not begin until late April.

Canada Wildrye.—As mentioned earlier, the species was apparently dying out of the seeded plots in 1953, the fourth year after seeding. It had been a very prominent member of the mixed seedings during 1951 and 1952 and when in flower, gave the appearance of a nearly pure stand in those plots subjected to one annual cutting. In 1953, it was almost entirely absent from the mixed plots, and although in somewhat better condition in the pure plots from which weekly collections were made, was not vigorous in any of the experi-

mental plots. Growth during 1953 was restricted to the peripheral regions of the crown. Only rare shoots or roots were developed in the central crown regions and, on many of the specimens, the older roots had apparently died without being replaced in this region, followed by fungal attack and decay of the crown tissues.

The fact that the woody stem bases formed in 1952 were not destroyed by burning in 1953, provided an opportunity for assessing the relative number of stems produced during each of these years. At the end of the 1953 season, a count of the current stems and burned stem bases of 30 plants showed 3.8 flowering stems per square inch of basal area in 1952 and only 0.8 in 1953, thus clearly indicating a marked decrease in vigor over the two years.

Clipping experiments

1953

The numbers of reproductive shoots when compared with the control plants, were apparently little affected by clipping in this experiment except for a decrease in reproductive stems in Indiangrass. The most generally consistent response to clipping as measured by counting individual shoots was an increase in the number of lateral shoots and thus, the number of total shoots per unit basal area. The shoot increase tended to be greatest on plants clipped at the low level or with removal of 75 per cent of the photosynthetic tissue. This was apparently not related to the number of stem apices which were removed, since the cut culms numbered approximately the same under both clipping levels at each site.

The seasonal pattern of the increase of shoots varied with the species. The greatest increase of the shoots of big bluestem and side-oats grama followed clippings made in July, with a gradual decline in numbers after this time, presumably due to the dying off of shoots at a rate more rapid than any increased shoot production. No increase in shoot number of little bluestem or Indiangrass occurred until after the August clippings at the Arboretum. No increase of any magnitude occurred in the shoots of Indiangrass at the West Hill Farm, where clipping of this species ceased prior to extensive stem elongation. The single midsummer clipping at the Arboretum resulted in a significantly large increase in lateral shoots only in big bluestem.

Until the last few clippings, side-oats grama was slower than the bluestem or Indiangrass to recover its original weight following the clippings at the West Hill Farm, where the date of clipping was determined by regrowth. The number of clippings made possible by this method of determination were 5 for Indiangrass, big bluestem and side-oats grama under 75 per cent removal and 7 for these 3 species under 35 per cent removal, while for little bluestem 6 clippings were made under 35 per cent removal and 8 under 50 per cent removal.

TABLE II. Total available carbohydrate analysis of crowns of West Hill Farm plants. Analysis and weights based on ten bunch samples

Species	Mg. TAC per sq. in basal area			Per cent of Control
	Control*	Clipping Level		
		35%	75%	
Side-oats Grama	121	91	..	75
	108	..	86	79
Indiangrass	119	94	..	80
	188	..	93	50
Little Bluestem	349	257	...	74
	346	...	193	56
Big Bluestem	298	265	...	89
	363	...	278	71

*Control for clipped plot on same horizontal line.

The results of the analysis of total available carbohydrates made on the crowns of plants at the Hill Farm are shown in Table II. Relative to control values, the absolute weights of carbohydrates per unit crown area of the bluestems and Indiangrass were reduced to a greater extent under 5 and 6 clippings removing 75 and 50 per cent of the photosynthetic tissue with each clipping than under 7 and 8 clippings removing 35 per cent. The amounts of reserves of side-oats grama were very similar under the two levels. Big bluestem plants under 35 per cent removal had higher absolute amounts of carbohydrates when compared with the control plants than did the other 3 species at this level of clipping, and neither clipping caused a great reduction in the reserves of this species. Clippings of 75 per cent and 50 per cent removal caused the carbohydrate contents of Indiangrass and little bluestem to be reduced to nearly 50 per cent of their respective controls.

Late in September, plants from the West Hill Farm plots under each clipping level were examined in the field and the laboratory. Under 75 per cent removal, the crowns of Indiangrass and side-oats grama showed indications of an accelerated deterioration which was not apparent on either species under 35 per cent removal clipping or on the control plants. Most of the cut floral stalks of big bluestem under both clippings possessed tertiary shoots, some as many as 5 per stem. Many of

these had 3 or 4 exserted leaves, but their axillary buds when compared with those of mature secondary shoots were approximately one-third the size of the latter and were green and succulent, whereas those on the latter were hard and brown.

1954

The data taken in 1954 (Table III) in the plots subjected to the greatest number of clippings reveal more precisely the effects of clipping these 4 species. Relative to the control values, the total shoot numbers of big bluestem were reduced highly significantly by any clipping, regardless of severity, the single midsummer clipping at the Arboretum causing as great a reduction in numbers as the 7 low level clippings. The relative reduction was less at the West Hill Farm than at the Arboretum, but was highly significant at both areas. The total shoot numbers of little bluestem at the West Hill Farm were somewhat increased over the control value. At the Arboretum, the shoots were highly significantly reduced in number in direct relation to the severity of cutting, the midsummer clipping resulting in the least reduction. It should be noted that this midsummer clipping was made at a time when all of the reproductive stems of big bluestem had elongated, but prior to elongation of all stems of little bluestem. Neither Indiangrass nor side-oats grama showed any consistent differences in the number of total shoots under any of the clippings, the only significant value being a reduction of shoots of Indiangrass under the high clipping at the Arboretum.

The average weights of aerial growth of these species (Table III) followed much the same pattern as shown by the foliage heights, in all instances being reduced below the weights of control plants in direct relation to the severity of clipping. The over-all weights of little bluestem and side-oats grama were the least reduced by clipping. However, the average weight of top growth per unit of crown area of side-oats grama was reduced to a greater extent by 5 clippings with removal of 75 per cent of the photosynthetic tissue than was that of any of the other species under this level of clipping at the West Hill Farm. The 7 mowings at 1½ inches at the Arboretum caused a great reduction in weight of the bluestems and Indiangrass and a lesser relative reduction of side-oats grama. A weight of top-growth of Indiangrass which exceeded that of control plants was found on plants subjected to single midsummer mowing.

When the values are further calculated as average weights per shoot, shown in the last column of Table III, some interesting differences appear.

TABLE III. Data taken in 1954 from control and plots clipped in 1953. Shoot numbers and foliage heights are averages of 30 bunches for each species; weights are averages of 5 bunches of each species

Species	Area[1]	Treatment	Shoots per square in.	Foliage height, inches	Foliage weight	
					gms. per 100 sq. in.	mg per shoot
Big Bluestem	WHF	Control	6.31	14	72	114
		35% cut	4.51**[2]	10	50	111
		75% cut	4.49**	9	45	100
	Arb	Control	8.93	18	126	141
		High cut	4.55**	11	53	116
		Low cut	5.01**	10	46	98
		Single	5.05**	13	79	156
Little Bluestem	WHF	Control	13.88	12	73	53
		35% cut	15.47	9	68	44
		75% cut	16.85*	9	62	37
	Arb	Control	11.44	17	73	64
		High cut	7.78**	11	59	76
		Low cut	6.53**	9	40	61
		Single	9.72**	14	66	68
Indian-grass	WHF	Control	2.97	14	41	138
		35% cut	2.63	11	24	91
		75% cut	2.53	10	26	102
	Arb	Control	2.51	18	38	151
		High cut	2.06**	10	27	131
		Low cut	2.58	10	14	54
		Single	2.53	16	44	173
Side-oats Grama	WHF	Control	4.94	8	24	49
		35% cut	5.19	8	22	42
		75% cut	5.19	7	13	25
	Arb	Control	5.56	11	44	79
		High cut	5.98	9	42	70
		Low cut	5.47	8	29	53
		Single	5.23	9	31	59

[1]WHF, West Hill Farm; Arb, Arboretum.
[2]Significant difference from control: (*) LSD at 5% level; (**) LSD at 1% level.

Although reduced in number below that of the control plants, the average weights of shoots of the bluestems relative to those of their respective controls were in general greater than those of the other two species. The average weight of shoots of Indiangrass under 7 low clippings at the Arboretum was particularly reduced, and the shoots of side-oats grama were of much lower average weight than those of their control plants under both the 75 per cent removal clippings and the 1½ inch clipping level.

DISCUSSION AND CONCLUSIONS

Increasing persistence of range and pasture grasses under defoliation is directly related to, (1) increasing possession of rhizomes (Weaver 1930), (2) increasing capacity for production of lateral shoots on unclipped plants (Stapledon 1928), (3) decreasing height and erectness of growth habit, (4) increasing lateness of seed germination and spring growth (Weaver and Dar-

land 1948), (5) decreasing growth rate (Weinmann 1948), (6) increasing fertile: sterile stem ratios, and (7) increasing lateness of elevation of the stem apex above the minimum point of grazing (Branson 1953). Branson suggests that the detrimental effects of removal of the stem apex may lie in the fact that decapitated shoots die, and thus reduce the photosynthetic area. The vegetative characteristics which have been correlated with relative persistence are related in one way or another to the degree to which the total foliage is made vulnerable to removal by clipping or grazing. Such decrease in photosynthetic area has been, both by inference and experimentation, related to reduction in development of the root system and the storage of reserve carbohydrates (Weinmann 1948). Varying with the species, the time, frequency and degree of defoliation have been found of great importance and, in general, the most frequent and severe clippings result in the greatest injury. Injury from defoliation also seems related to the duration of the pre-flowering vegetative period, when expansive growth is extremely rapid (Rappe 1951). Following onset of the reproductive phase, vegetative growth slows and regrowth following clipping becomes less rapid.

The results of the present investigation of the six prairie grasses support the above generalizations. The most persistent of these species, side-oats grama, is of small stature, rhizomatous, and highly productive of lateral shoots when unclipped, and, relative to the other five species, has a low fertile: sterile stem ratio and a slow growth rate. The "decreasers," big bluestem, little bluestem, switchgrass, Indiangrass and Canada wildrye, possess characteristics which are opposed to those of side-oat grama and, in general, are tall and erect, produce few lateral shoots, and have high fertile: sterile stem ratios.

When plots of these grasses were cut between 1½ and 2 inches from the ground (essentially the clipping height used in the 1949-1952 experiment), side-oats grama was found to lose between 15 and 40 per cent less photosynthetic tissue than did the tall and mid grasses. This, alone, would seem sufficient general explanation for the success of side-oats grama in areas of the tall grass prairie subjected to grazing which is intensive from the standpoint of the total species composition. With such relatively moderate losses of photosynthetic tissue, side-oats grama would be expected to show little injury and would benefit from the reduction of competition from the decreasing taller grasses. When this species was subjected to defoliation levels as severe as those suffered by the taller grasses under the 1½ inch clipping (*i.e.*, 75 per cent removal clipping), it was similarly weakened.

For purposes of soil conservation and forage use, it seems desirable at times to maintain vigorous stands of the prairie grass "decreasers" in their areas of adaptation. Were the reduction of photosynthetic area alone involved in weakening stands of these plants, it would seem that their decline could be obviated by maintaining grazing pressure at levels at which excessive amounts of photosynthetic tissue would not be removed. These data would seem to indicate that this, indeed, would be true of Indiangrass and side-oats grama, as the absolute carbohydrate contents of Indiangrass in 1953, and the height and weight of the top-growth of both species in 1954 were reduced in direct relation to the severity of clipping during 1953. The carbohydrates of side-oats grama were reduced by seven 35 per cent removal clippings to the same extent as by five 75 per cent removal clippings, but this similarity was not evident in 1954. The weight of foliage in 1953 of Indiangrass plants subjected to one annual midsummer clipping exceeded that of control plants and vigorous stands of this species have been observed in areas of southern Wisconsin which have been mowed once annually for many years.

Further factors, however, appear operative in the responses to clipping of the other four species. Under seven 35 per cent removal clippings at the West Hill Farm in 1953, the absolute amounts of carbohydrate reserves in big bluestem suffered less relative reduction than did those of the other species. Weaver and Zink (1946) report 81 per cent of banded roots of big bluestem alive 3 years after banding, while only 14 per cent remained alive on side-oats grama at the end of this time. Such differences in root longevity were noted in the current work and may account for some of the difference in the amounts of stored carbohydrates of the plants, since much of the sample tissue of the bluestems was produced during the preceding season, while that of side-oats grama and Indiangrass was largely formed during 1953. It would seem, however, that the food storage of big bluestem was not reduced during one season of clipping to a degree compatible with its rapid decreaser status.

Big bluestem produced no overwintering primary shoots, all aerial shoots in 1953 developing from basal buds. Few or no tertiary shoots developed on unclipped plants during the 1953 season, the basal buds of the original secondary shoots apparently remaining dormant, a characteristic also noted by Mueller (1941). Yet, clipping of this species following the start of floral shoot elongation resulted in a great increase of lateral

shoots on plants under all levels of defoliation, the single midsummer clipping causing an increase equal in magnitude to that on plants clipped all season. The buds of lateral tertiary shoots which developed under clipping in 1953 seemed neither mature nor dormant in late autumn. The shoot number on all clipped plants was highly significantly lower than on control plants in 1954, the reduction on plants clipped once, again, equalling that on plants clipped all season. It is suggested here that the rapid decrease of big bluestem is directly related to a lowered number of dormant buds on plants which have been clipped or grazed, and thus a reduced shoot production per unit crown area in the following season. Continued clipping or grazing of this reduced shoot number during subsequent years could be expected to further reduce the photosynthetic area and to eventually be accompanied by impaired root production and food storage, thus accelerating the decline of the species. Conversely, a rapid recovery under a lack of subsequent defoliation is suggested by the lack of excessive reserve reduction in 1953, and the vigorous condition of the shoots which developed in 1954. It may be such a capacity for rapid recovery that allows the successful persistence of big bluestem under deferred and rotational grazing plans.

Much the same responses might be expected from little bluestem were it not for certain differences in the life histories of the two species. Due to a later flowering date, the stem apices of little bluestem were susceptible to removal later in the season than those of big bluestem. A reduced shoot number was found in 1954 only on those plants of little bluestem which had been stimulated to increased lateral branching in 1953. The greatest shoot increase occurred on plants cut in late August and early September at the low level at the Arboretum, followed by those cut at the high level and those cut once in midseason, and the relative shoot reductions in 1954 were in this same order. The last two cuttings at the Arboretum followed elongation of nearly all floral stalks above the level of mowing, while the midseason clipping preceded this stage, some inflorescences being developed on the regrowth following this clipping. At the West Hill Farm where all clipping ceased prior to stem elongation of little bluestem, the shoot numbers were not reduced in 1953 and were significantly increased in 1954. Branson states that while the very high fertile: sterile stem ratio of little bluestem would cause it to be expected to decrease more rapidly than other grasses, the abundance of old stems seemed to discourage grazing and caused it to persist somewhat longer. Since this greater persistence is also found in clipping experiments, it may be suggested that this is, in addition, related to the lateness of stem elongation and flowering in that large numbers of stem apices are not removed unless clipping or grazing occurs late in the season. The moderately long life of the root system and the high weight per shoot even when the shoot numbers were reduced, suggest that this species also possesses a high capacity for recovery from one season of heavy grazing.

Clipping treatments were not imposed on switchgrass, but its rapid decline under defoliation would seem directly related to the elongation of all stems during the season, and to a paucity of basal shoots and foliage. Any clipping or grazing after elongation had begun would remove not only all of the stem apices, but in addition most of the photosynthetic tissue. Lateral shoots may be developed, but would seem unlikely to be able to provide adequate photosynthetic tissue for subsequent growth and storage.

The decline of Canada wildrye in both the clipped and control plots is in agreement with the observations made by Weaver and Zink, who state that it is indicated to be a species that depends for permanency of occupation more upon rapid reproduction by seed than upon length of life of the individual. Its success under one annual midsummer clipping during the earlier experiment was probably due to the fact that this clipping was made at anthesis of big bluestem, Indiangrass and switchgrass, at which time the cool season wild rye was mature and the fruit ripened.

The tall grasses presumably persisted for centuries under grazing by bison and other wild herbivores, only to decline under grazing by domestic animals. The success of the grasses, particularly the bluestems, may have been related to the migratory habits of the majority of the native animals and to the availability of unrestricted range, both factors resulting in a lack of annual defoliation of each bunch or sod, and a lack of continuous severe defoliation of any one plant. The dynamically stable botanical composition of the Prairie would then tend to be maintained even while supporting relatively large numbers of grazing animals.

Summary

Among the native grasses of the Tall Grass Prairie, *Andropogon gerardi, Panicum virgatum, Elymus canadensis, Sorghastrum nutans,* and *Andropogon scoparius* have been found to decrease in density in direct relation to increases in the intensity of grazing or clipping, in that relative order, while *Bouteloua curtipendula* at first increases, and then decreases as defoliation becomes

severe. In the attempt to ascertain the autecological factors related to these differential responses, studies were made on these species in established plots at the University of Wisconsin during 1953 and 1954. Data were obtained on the life history and general morphology of each species and each was subjected to clipping treatments removing varying amounts of photosynthetic tissue.

The "increaser" status of *B. curtipendula* under grazing of mixed stands is believed to be related to the low amounts of photosynthetic tissue removed from this short, rhizomatous plant, at the same time the taller, more erect species suffer excessive losses and are rapidly weakened. *B. curtipendula* was similarly weakened by severe losses photosynthetic tissue, but possessed somewhat greater resistance due to a low vegetative: reproductive shoot ratio, an early flowering date and a slow growth rate. The decreases in density of *S. nutans* and *B. curtipendula* under grazing or severe clipping appear to be due to the reduction in photosynthetic tissue and stored food reserves.

This same decrease in vigor correspondent to decreases in photosynthetic tissue was found with the other species, but further factors appeared operative in their responses. The more rapid decline of *A. gerardi* was indicated to be related to production of a relatively inflexible number of shoots and dormant buds in any one season, to stimulation of shoot development by the latter under clipping, and to a resultant reduction of shoot numbers in the following years. Clipping of *A. scoparius* late in the season resulted in similar responses, but its general reaction was modified by the late flowering date of the species. Due to elongation of all shoots of *P. virgatum* during the season and to a lack of basal foliage, any clipping or grazing would remove all stem apices and most of the photosynthetic tissue, contributing to its rapid decline. Since *E. canadensis* was dying out of the five-year-old plots, it was not subjected to clipping treatments. Data are presented indicating the extent of this decline.

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SPROUTING OF BITTERBRUSH (*PURSHIA TRIDENTATA*) FOLLOWING BURNING OR TOP REMOVAL

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Bitterbrush (*Purshia tridentata* (Pursh) DC.) is one of the most widely distributed of all western shrubs, ranging from British Columbia and Montana to California and New Mexico. Because it is abundant on many portions of its extensive range and because it is a valuable forage plant for both domestic livestock and big game, it is one of the most important browse species (U. S. Forest Service 1937). In recent years, bitterbrush has attracted additional interest because it appears to have excellent possibilities for revegetating depleted winter deer range in many parts of the West (Holmgren 1954).

Since it is commonly associated with big sage-

brush (*Artemisia tridentata* Nutt.), much bitterbrush has been burned during recent years as a result of the widespread use of fire for sagebrush eradication (Blaisdell 1953, Pechanec *et al.* 1954). Billings (1952) has reported that bitterbrush "is generally eradicated permanently by fire in the western Great Basin because it rarely root-sprouts in that region and its seeds are not particularly mobile." Hormay (1943) stated that "hundreds of thousands of acres of bitterbrush have been destroyed by fire" in California and that "only two instances of sprouting after burning have been observed."

Sprouting of bitterbrush from the base of the stem (root crown) following burning in eastern Idaho, however, is a common occurrence. For example, on one large experimental burn on the Upper Snake River Plains, 49 per cent of the plants sprouted on the lightly burned portion, 43 per cent on the moderate burn, and 19 per cent on the heavy burn (Blaisdell 1953). Considerable bitterbrush sprouting has been observed on two burns in southwestern Idaho by Ralph Holmgren and on one burn in eastern Washington by George Garrison (personal communications). Also, the authors have seen a limited amount of sprouting in central and northern Utah.

Since sprouting is very important in the maintenance of satisfactory stands of bitterbrush, a preliminary study was initiated in the spring of 1953 at the U. S. Sheep Experiment Station near Dubois, Idaho, to provide more information on this phenomenon.

The topography of the study area is similar to much of the Snake River Plains, having little surface drainage and slight relief except for outcrops of Pleistocene basaltic lava. The sandy-loam soil varies in depth from more than 3 feet in the swales to a very shallow or no covering on the lava ridges. Precipitation averages about 11 inches annually and except for a slight concentration in May and June is rather evenly distributed throughout the year. Temperatures may reach a maximum of 100° F. in summer and a minimum of —30° F. in winter. The frost-free period averages 120 days, with the last spring frost occurring in May or June and the first fall frost in September or October. Soil moisture of the surface 18 inches generally falls below the wilting coefficient in late June or early July. Growth of grasses and forbs ceases at this time, but shrub twigs and flower stalks may continue to grow until early August.

During the years in which the study was conducted, 1953 and 1954, precipitation was only about 75 per cent of normal. Mean temperatures during the spring of 1953 were considerably below normal, but during the remainder of the 2-year period, temperatures were generally higher than normal.

The natural vegetation is predominantly shrubs with an understory of perennial grasses and forbs. Sagebrush (*Artemisia tripartita* Rydb. and *A. tridentata* Nutt.) is by far the most abundant of the shrubs, but bitterbrush is very common, particularly in swales where it is often the dominant species. Bluebunch wheatgrass (*Agropyron spicatum* (Pursh) Scribn. and Smith) is the most abundant of the grasses, and arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.), of the forbs. A large variety of grasses, forbs, and shrubs are present in lesser amounts. Cheatgrass (*Bromus tectorum* L.), an annual associated with frequent fires and very common on many portions of the Snake River Plains, is virtually nonexistent here.

Methods

The study was designed to ascertain the relative effects of fire and complete top removal by clipping on subsequent sprouting of bitterbrush, as well as the effect of time of destruction.

An area along the border of a burn made in 1939 was divided into 7 blocks, and within each block 40 bitterbrush plants were selected for study. Of these, 20 were located on the 1939 burn and 20 on the adjacent range which showed no indication of previous burning. Most of the plants selected on the old burn were apparently sprouts from bushes whose tops were killed by fire in 1939, since pieces of charred wood were still attached to many of them. Treatments were applied at each of 6 dates (the middle of each month, May through October) to 1 of 6 blocks selected at random. Of the 20 plants in each block located on the old burn, 10 were burned and 10 were cut off 2 inches above the ground level; the 20 plants on the previously unburned portion were treated similarly. It was possible to burn entire areas containing plants to be so treated on the previously unburned portion of the blocks, but the lower density of shrubby vegetation on the 1939 burn necessitated burning individual bitterbrush plants with a weed burner. The seventh block was reserved as an untreated check.

At various times after treatment in 1953 and during the 1954 season, observations were made of the manner in which sprouting occurred, number of plants that sprouted, and degree of survival.

Results

Bitterbrush sprouts on both burned and severed plants were found to originate in two different

ways: from an existing mass of dormant buds wholly or partly encircling the stem at ground level (Fig. 1) or from a callus of meristematic tissue formed beneath the bark after treatment and encircling the stem, usually about an inch above (but occasionally just below) ground level (Fig. 2). The bud mass was often partially buried by soil, and sprouts which appeared after burning were usually from these protected portions. Similarly, the callus of meristematic tissue was formed on stems protected by heavy bark or soil, particularly on the less severely burned plants. Although possible damage to the plants prevented accurate determination of sprout origin in some cases, it appeared that sprouting of burned plants was mainly from the newly formed callus. Sprouts from plants whose tops were severed originated in both ways, but in contrast to burned plants development from existing dormant buds was the more common. Such sprouts grew rapidly, and some plants clipped in the spring produced a considerable volume of herbage by fall (Fig. 3).

FIG. 1. A bitterbrush plant in August 1953, on an area burned in August, 1952, showing vigorous sprouts from a large dormant bud mass. Sprouts originate from the undamaged portion at or below the soil level indicated by toothpick. Above ground buds are badly charred and apparently dead.

FIG. 2. Two bushes as they appeared on August 3 after burning on May 15. Bark has been stripped off to expose a callus formed just above ground level (indicated by pencil). The plant on the right has produced sprouts more than an inch long.

FIG. 3. A bitterbrush plant severed 2 inches above ground level on May 15 as it appeared on August 3. Sprouts average about 12 inches in length.

Sprouting was observed as early as 3 weeks and as late as 13 months after burning or clipping. For example, out of 40 plants treated on July 15, 16 had sprouted by August 5. On the other hand, 4 of the 40 bushes treated in August, 1953, did not sprout until September, 1954. Three of these were bushes that had been burned, and one was a bush whose top had been severed. As might be expected, sprouts from existing dormant buds usually appeared earlier than sprouts from the callus beneath the bark; consequently, the former produced a greater volume of herbage during the first year (Fig. 4).

FIG. 4. Bitterbrush plants approximately one year after burning. Plant on the right sprouted from undamaged dormant buds below soil surface; plant on left sprouted from a callus formed beneath the bark.

Of a total of 240 bitterbrush plants whose tops were killed by burning or clipping, 146 or about 60 per cent sprouted (Table I). Sixty bushes, exactly 50 per cent, of those burned produced sprouts; whereas 86, nearly 72 per cent, of the bushes sprouted following clipping.

TABLE I. Number of bitterbrush plants that sprouted following burning or top removal by clipping at 6 dates during 1953, and survival as of September 1954

Treatment date*	1939 burn			Previously unburned			Totals		
	Burned	Clipped	Sub-total	Burned	Clipped	Sub-total	Burned	Clipped	Grand total
	(Number of plants that sprouted following treatment in 1953)								
May 13	8	8	16	7	5	12	15	13	28
June 15	7	9	16	6	4	10	13	13	26
July 15	6	9	15	2	4	6	8	13	21
Aug. 13	4	10	14	7	5	12	11	15	26
Sept. 15	4	10	14	2	7	9	6	17	23
Oct. 14	6	9	15	1	6	7	7	15	22
Total	35	55	90	25	31	56	60	86	146
	(Number of sprouting bitterbrush plants alive on Sept. 20, 1954)								
May 13	2	6	8	6	4	10	8	10	18
June 15	2	6	8	2	0	2	4	6	10
July 15	4	8	12	1	1	2	5	9	14
Aug. 13	4	8	12	6	4	10	10	12	22
Sept. 15	4	10	14	2	6	8	6	16	22
Oct. 14	6	9	15	1	6	7	7	15	22
Total	22	47	69	18	21	39	40	68	108

*A total of 40 plants were treated at each date, 10 in each of the 4 categories.

Date of treatment had little effect on number of plants that sprouted following clipping, but burning in May and June caused more sprouting than in the other months (Table I). The exceptionally high amount of sprouting following burning in August on the previously unburned area should be discounted as it is probably the result of inadvertently spraying these bushes with water while attempting to prevent spread of the fire. Bushes that were burned later than July or clipped later than August did not sprout until the following growing season.

At every date, there was more sprouting of bitterbrush plants on the 1939 burn than on the previously unburned area. A total of 90 bushes (75 per cent) sprouted on the old burn, whereas only 56 (less than 50 per cent) sprouted on the previously unburned area.

There was a fairly high mortality of the plants that sprouted following burning or top removal. Only 108 of the original 146 sprouting plants were still alive on September 20, 1954 (Table I). Losses were particularly heavy during the winter among sprouts from the May and June treatments. Apparently ultimate survival may be low in spite of a high degree of sprouting initially. Losses were greater among sprouts from burned than from severed plants, average mortalities being 33 and 21 per cent, respectively. During the period of study, there were no losses among the 40 plants on the block reserved as an untreated control.

Utilization of the bitterbrush sprouts by sheep and rabbits was fairly heavy during the late fall of 1953. At this time, practically all of the forage on the study area was dry, and the relatively green, tender shoots were apparently the most palatable forage available. Although mortality during the ensuing winter of the plants subjected to moderate and heavy utilization was only slightly higher than of plants grazed lightly or not at all, rate of recovery from burning or top removal was undoubtedly retarded by grazing.

DISCUSSION

Sprouting of bitterbrush following burning or top removal is apparently influenced by a number of factors, but unfortunately this preliminary study does not allow a clear separation of their relative importance. Since it has been previously ascertained that degree of sprouting is strongly affected by burn intensity (Blaisdell 1953) no attempt was made to provide further information on this subject. However, intensity was difficult to control, and it was noticeable that bushes burned early in the season were apparently damaged less than others, probably because of the less intense burn obtained at that time. At any rate, burn intensity must be considered when attempting to evaluate the effect of other factors on sprouting of bitterbrush. It appears that damage to the stem in the region where sprouting normally occurs (about a 3-inch section 1½ inches above and below ground level) is the chief reason why less sprouting usually occurs after burning than after complete top removal. That bitterbrush rarely, if ever, sprouts below this region was demonstrated during a supplementary study by cutting 40 plants about an inch beneath the soil surface and noting that only 3 of these were able to sprout.

Since date of top severance had little effect on amount of sprouting, it appears that date of burning is important only as it affects intensity or degree of damage to the base of the stem. As the season progresses, fuel moisture diminishes in both the living plants and litter, producing hotter and hotter fires. Likewise, soil moisture normally de-

creases, allowing more charring of the stem at and just below ground level. For example, during 1953, soil moisture in the surface 18 inches diminished from about 18 per cent in May and June to less than 7 per cent in October. As already mentioned, the relatively high amount of sprouting following the August burn on the previously unburned area is probably the result of spraying a considerable quantity of water on the burned bushes while attempting to confine the fire to the specified block.

The much higher rate of sprouting on the old burn than on the previously unburned area may be due to several factors. In the case of burned plants, it is possible that intensity may have been important as more fuel was generally present on the previously unburned portion of the block and in many instances these fires apeared to be hotter than those on the old burn. However, the fact that sprouting following clipping was also much higher on the old burn indicates that intensity may not be the primary factor in this instance. A real possibility for the differences in degree of sprouting is the difference in ages of bitterbrush plants on the previously burned and unburned areas. Those on the 1939 burn were either sprouts whose tops were less than 15 years old or new plants even younger, whereas those on the unburned area were of mixed ages averaging about 30 years. Perhaps younger and possibly more vigorous bushes sprout more readily than older ones. As a matter of fact, 7 of 10 clipped plants under 15 years of age on the previously unburned area sprouted, whereas only 24 of 50 sprouted among those older than 15 years.

It is also possible that bitterbrush sprouting is related to inherent qualities of particular plants and that the 1939 burn, because of natural selection, actually contains a higher percentage of potential sprouters than the unburned area. Some support is given the theory that sprouting is influenced by genetic factors because of the large geographical area (the western Great Basin and California) where scarcely any bitterbrush sprouting has been observed. It seems hardly credible that environmental factors over such a large area would be so consistently unfavorable that bitterbrush sprouting could be almost entirely excluded.

Supplementary Observations

In an effort to determine relative abundance of plants with an existing mass of dormant buds (Fig. 5) and the importance of such buds in producing sprouts following burning, 120 bushes were examined during the fall of 1954 on a 1,000-acre area burned the previous year. Sixty-three per cent of the bushes sprouted—24 per cent from existing buds and 39 per cent from the callus developed beneath the bark after burning. Since the dormant bud masses were present on 70 per cent of the plants, it appears that in many cases the existing buds were killed by the fire, and sprouting was then entirely dependent upon formation of new buds on the meristematic callus.

Fig. 5. Two unburned bitterbrush. The one on the right has a typical mass of dormant buds which may produce sprouts following burning or top removal. Pencil points to ground level.

Apparently dormant bud masses are much more effective in providing a means of sprouting following top removal by clipping, since more than half of the sprouting of clipped plants on the experimental area originated from existing buds.

Although from one-third to two-thirds of the bitterbrush plants usually sprout after burning on the Upper Snake River Plains, there is at least one instance of a large burn on which survival was very low. This burn is in an area where much bitterbrush sprouting has occurred at other times, and reasons for this high mortality are not known. It indicates the importance of environment, even though sprouting of bitterbrush may be partially controlled by inherent factors.

Summary

Much bitterbrush, one of the most important browse species on western ranges, has been burned in recent years, chiefly as a result of widespread use of fire for sagebrush eradication. Although scarcely any sprouting of bitterbrush has been observed in the western Great Basin and California, sprouting from the root crown following burning is common in eastern Idaho. Because of the importance of sprouting in the maintenance of satisfactory stands of bitterbrush, a study was made on the Upper Snake River Plains of the relative

effects of fire and complete top removal on this phenomenon.

Bitterbrush sprouts on both burned and severed plants originated in two different ways: from an existing mass of dormant buds wholly or partly encircling the stem at ground level or from a callus of meristematic tissue formed beneath the bark after treatment and encircling the stem.

Fifty per cent of the burned plants produced sprouts, whereas nearly 72 per cent of the bushes sprouted following top removal by clipping.

Date of treatment had litle effect on number of plants which sprouted following clipping, but burning in May and June resulted in more sprouting than in other months.

At every date, more bushes sprouted on the former burn than on the previously unburned area.

There was a fairly high mortality of plants which sprouted following both burning and top removal, and losses were greater among sprouts from burned than from severed plants.

An examination of a large burn indicated that domant bud masses were present on 70 per cent of the bitterbrush, but many of these had been killed by fire. Nearly twice as many plants sprouted from the callus formed beneath the bark as from existing buds.

This study suggests that sprouting of bitterbrush is influenced by both genetic and environmental factors. Burn intensity strongly affects sprouting, but date of burning appears important only as it causes differences in intensity.

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COMPETITION BETWEEN ANNUALS AND YOUNG BITTERBRUSH (*PURSHIA TRIDENTATA*) IN IDAHO[1]

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On large areas of important big-game winter range in southwestern Idaho, a once-productive shrub cover is now so depleted that restoration of browse within a reasonable time appears to be attainable only by artificial measures. Of several browse species known to be adapted for survival on these ranges, bitterbrush (*Purshia tridentata* (Pursh) DC.) shows by far the most promise of being useful for artificial range rehabilitation (Holmgren 1954). It has been planted in experimental plots or in large-scale range reseeding projects on one or more sites in southwestern Idaho almost every year since 1937. The success of these seedings varied; some are now well-established stands, whereas others—in fact, the majority—are total or near failures. Causes of the failures are in most cases conjectural; it is known only that the stands were either initially very poor or lacking, or that very high mortality occurred in the better seedling stands during the first year or so after germination. Possible explanations for poor initial stands might be low-quality seed, seed-gathering rodents, or improper planting techniques. Failure of initially good seedling stands to become established might be attributed to any one or a combination of several factors, among which freezing, frost-heaving, damping-off, drought, insect and rodent depredations, trampling and grazing by game and livestock, and competition with other vegetation could have been important. The studies described in this report were made to ascertain the effect of other vegetation, especially cheatgrass (*Bromus tectorum* L.), on survival and establishment of bitterbrush seedlings. They constituted a phase of a cooperative interagency big-game winter range browse restoration research program.

The success with which cheatgrass competes with slow-growing or spring-germinating weeds or perennial grasses is well-known (Piemeisel

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1951, Stewart and Hull 1949). By the time bitterbrush seed germinates in the spring, numerous fibrous roots of cheatgrass, a winter annual, have quite thoroughly interpenetrated the upper several inches of soil, and moisture in that zone is already being drawn on heavily (Robertson and Pearse 1945). In California, Hormay (1943) observed that cheatgrass retarded the natural establishment of bitterbrush. The influence of cheatgrass and other annual vegetation on establishment, growth, and survival of artificially seeded bitterbrush has not been described heretofore.

The Study Areas

Most of the study areas were on the deer winter range along the South Fork of the Payette River in southwestern Idaho. This range consists mainly of south exposures with slope gradients between 15 and 70 per cent. Its granitic soil is loose and coarse and has a low moisture-retaining capacity. Average annual precipitation is about 22 inches, most of it falling in winter as snow. The small amount of summer precipitation generally occurs as infrequent, scattered, high-intensity thundershowers. An annual type vegetation predominates; in most years it is almost exclusively cheatgrass, but broad-leaved weeds such as groundsmoke (*Gayophytum diffusum* T. & G.), prickly lettuce (*Lactuca scariola integrata* Gren. & Godr.), and knotweed (*Polygonum douglasii* Greene) are occasionally dominant on much of the area, especially in poor cheatgrass years.

Study areas near the South Fork of the Boise River are similar in soil, topography, and climate to those along the Payette.

First Growing Season

To observe the response of bitterbrush seedlings under 3 degrees or kinds of plant competition, 3 cultural treatments were applied to 6 plots on a typical south-facing cheatgrass site on the Payette range.

Two plots were disked in May, 1949, to destroy the cheatgrass cover before seed was formed. Weeds that appeared in subsequent seasons through 1952 were hoed out. Two other plots were disked but no further effort was made to keep weeds out. In 1950, there was a vigorous stand of spring-germinated broad-leaved annuals on these plots; cheatgrass had been practically eliminated. In 1951 and 1952, weeds were more numerous than in 1950, and in 1952 cheatgrass was again the dominant species. In the third set of 2 plots, the only disturbance of the original cover was that small amount associated with the planting of bitterbrush seed. These plots remained almost pure cheatgrass, with only a few low-vigor broad-leaved weeds present in the stand.

Fig. 1. Bitterbrush seedlings under three kinds of weedy competition: (A) in cheatgrass—this seedling is dead, (B) among broad-leaved annual weeds, (C) with all weeds kept out. Photos taken August 30, 1950, the first growing season. (F-472792, F-472793, F-472791)

Bitterbrush was hand-seeded in each plot in November, 1949, in 3 shallow furrows 20 feet long,

spaced 2 feet apart. The amount of seed per row and its uniformity of distribution were not controlled by accurate measurement. The seeds were covered with about one-half inch of soil. On May 10, 1950, there were 1.98, 2.10, and 2.80 newly emerged bitterbrush seedlings per average foot of row in the weed-free, broad-leaved weed, and cheatgrass plots, respectively.

Differences in growth rate and survival of bitterbrush that could be associated with plot treatment first became apparent in early summer. Table I shows the percentage survival of bitterbrush through the first year under the different plot treatments. Conditions were most favorable for survival and growth on the weedfree plots, and severest on the cheatgrass plots, where all seedlings died before the end of August (Fig. 1).

Cheatgrass grew most rapidly in May and early June, just before it matured seed and died. During the same period, the broad-leaved weeds in plots given the second treatment were still very small, and exhibited no competitive effect on the young bitterbrush (Table I). These weeds, with taproot systems paralleling the development of seedling bitterbrush roots (Spence 1937), continued to grow all summer, however, and by mid-September survival of bitterbrush among them was only about two-thirds that in plots free of all weedy competition. The higher rate of bitterbrush mortality associated with weedy competition continued through the fall and winter. On the weedy plots, 17 per cent of the seedlings alive in September were dead by the following spring, while among the more vigorous bitterbrush on the clean plots mortality for the same period was only 3 per cent.

TABLE I. Percentage survival of bitterbrush seedlings under three kinds of weedy competition, based on original counts made May 10, 1950

Treatment	Survival through:		
	June 24, 1950	Sept. 18, 1950	May 16, 1951
	Per cent		
1. No weeds	90	68	66
2. Broad-leaved weeds	91	48	40
3. Cheatgrass	46	0	..

Differences in first-year growth of bitterbrush under the two treatments where it survived are shown in Table II. The figures for each treatment were derived from twenty plants randomly selected and clipped at ground level in November, 1950. The vigorous, well-branched plants in the weed-free plots had an average weight about 26 times greater than the small, weak-stemmed seedlings in the weedy plots. Since survival was better there, too, total bitterbrush yield on the weed-free plots was estimated to be about 35 times greater than on the plots not weeded.

TABLE II. Average size of bitterbrush seedlings at the close of the first growing season. November 1950

	Treatment 1 No weeds	Treatment 2 Broad-leaved weeds
Air-dry weight of leaves and stems	2.6 grams	0.1 gram
Height	5.8 inches	0.9 inch
Number of stems more than ½-inch long	5.5	1.1

SECOND AND THIRD GROWING SEASONS

In 1951, the second growing season, one-half of each weedy plot was weeded, while half of each clean plot was allowed to revert to weeds. In the latter half-plots, the weeds that came in were of the broad-leaved type, in an open stand that grew vigorously all summer. In 1952, weeds were considerably more abundant on them but were mostly of the same summer-annual, broad-leaved type. The weeded half-plots on the originally weedy treatment were kept clear of weeds during the 1951 season only. The inhibiting effect of weedy competition on growth rate of second season bitterbrush was evidenced in two ways by this partial reversal of treatments (Table III). Growth rate was reduced where weeds invaded what had been weed-free plots the first season, and release by removal of weeds after one year's growth in competition with weeds resulted in a marked increase in growth rate as compared to where weedy competition was never eliminated.

In Table IV, which is in part a continuation of Table I, are shown survival percentages of bitter-

TABLE III. Average size of bitterbrush plants, second and third growing seasons*

Treatment	Average height			Average crown diameter		Estimated average current season twig-leaf yield	
	Apr. 1951	Nov. 1951	Dec. 1952	Nov. 1951	Dec. 1952	1951	1952
	Inches			Inches		Grams, green	
Weed-free 3 seasons	5.5	15.4	18.8	10.8	15.1	60.3	58.8
Weed-free 1st season only (1950)	5.2	11.7	15.2	7.0	10.4	16.6	17.1
Weed-free 2nd season only (1951)	1.3	7.5	11.7	3.6	7.3	8.2	8.7
Weedy 3 seasons	1.3	4.2	8.7	1.7	4.8	1.3	3.8

*Twenty plants were marked for measurement in April 1951, but mortality between then and December, 1952, reduced the number of marked plants to 17, 19, 14, and 12 for lines 1, 2, 3, and 4, respectively. Averages are derived from measurements and estimates of marked plants alive on date of observation.

brush under the various conditions of weedy competition. These percentages are based on the original seedling stands counted May 10, 1950, with adjustments made for the plants clipped the first fall. Survival through the first three growing seasons appears to be directly related to the vigor attained by the seedlings in their first growing season—vigor evinced by the sizes shown in Table II. The vigorous seedlings on plots that were weed-free the first growing season suffered negligible mortality in subsequent seasons, even where weeds were allowed to reinvade. The suppressed seedlings in the weedy plots, on the other hand, continued to die off into their third growing season. This suggests that success of bitterbrush seedings might be known from sample counts made at the end of the first year if the plants have grown vigorously, as those growing in the absence of weeds did, but where association with annual weeds has suppressed bitterbrush seedling growth, the success of establishment cannot be determined for a number of years.

TABLE IV. Percentage survival of bitterbrush, second and third growing seasons, under varying conditions of weedy competition, based on original seedling counts of May 10, 1950

Treatment	Per cent survival through:			
	May 1951	Nov. 1951	May 1952	Dec. 1952
Weed-free 3 seasons	66	66	62*	55*
Weed-free 1st season only (1950)	66	64	58*	51*
Weed-free 2nd season only (1951)	40	36	29	26
Weedy 3 seasons	40	34	27	14

*Gopher activity during winter of 1951-1952 was the sole cause of mortality indicated in columns 4 and 5, lines 1 and 2. No gopher activity was noted in plots of the other 2 treatments.

ADDITIONAL EVIDENCE

On a weed-free area near the plots discussed above, 80 per cent of an initial seedling stand of 165 bitterbrush seedlings were alive on August 10, 1950, the first growing season. All these plants survived the following winter. In April, 1951, the area was divided into 8 equal parts, 4 of which were weeded, and 4 allowed to revert to weeds. In 1952, none of the 8 plots was weeded. The bitterbrush plants were measured in August, 1950, again in May, 1951, after the area was divided, and at the close of the 1951, 1952, and 1953 growing seasons. No mortality occurred until the winter of 1951-52, when pocket gophers became active in some of the plots. Severe defoliation by grasshoppers in the summer of 1952 and gopher activity the following winter were the apparent causes of further mortality. In no instance was any bitterbrush plant lost because of apparent drought or competition for moisture. By the end of 1953, 75 per cent of the stand counted in August, 1950, was still alive and vigorous.

Average sizes of plants under the two treatments at several dates are shown in Table V. The invasion of weeds into plots after one season of growth free of weedy competition resulted in a slower growth rate of young bitterbrush there than on plots where weeds were kept out in the second season. The presence of weeds affected the plant form as well. Those second-season bitterbrush plants growing in association with tall broad-leaved weeds developed a more upright habit than those growing in the open. The latter were rounded, and several branches spread horizontally near the ground, whereas the branches of the former were all either vertical or ascending. The average estimated weight of herbage produced by bitterbrush plants on weedy plots in 1951 was 28 per cent of that on weed-free plots. This figure is the same as that derived from the same second-season treatment-comparison in the plots first discussed above.

TABLE V. Growth of bitterbrush under two conditions of association with weeds

	Treatment	
	Weed-free 1950 Weedy 1951-1953	Weed-free 1950-51 Weedy 1952-1953
	Average height (inches)	
Aug. 1950	5.2	5.4
May 1951	9.8	9.6
Nov. 1951	13.8	18.9
Sept. 1952	16.9	21.8
Nov. 1953	18.9	26.5
	Average crown diameter (inches)	
Aug. 1950	3.4	3.5
May 1951	9.4	10.1
Nov. 1951	11.1	19.3
Sept. 1952	16.5	26.1
Nov. 1953	21.5	32.1
	Average estimated current season's twig-leaf production (grams, fresh weight)	
Nov. 1951	85	300

METHODS AND DEGREES OF CHEATGRASS ERADICATION

Within an area about 200 feet across on the Payette game winter range, 5 sets of 8 circular plots were hoed shortly after cheatgrass had germinated in October, 1950. The plots were 1, 1½, 2½, and 4 feet in diameter, with 2 plots of each size in each set. One plot of each size was kept

clear of weeds by hoeing the following year; the other was not. Immediately after the plots were prepared, 12 sound-appearing bitterbrush seeds were planted singly at a depth of approximately one-half inch in the central 80 or so square inches of each of these plots and in a ninth plot, that had not been weeded, in each of the 5 sets.

Weeds were counted in May, 1951. On the plots that had been hoed in the fall, there was an average of 34.8 weeds per square foot, almost exclusively cheatgrass, while on comparable plots which had not been hoed, the average number of weeds was 14 per square foot. The difference between mean weed numbers was highly significant. The counts suggest that fall germination of cheatgrass was far from complete, and that such plants as did germinate then may have inhibited subsequent germination, or establishment from seeds germinating later. Removal of the fall-germinating cheatgrass by hoeing seems to have made possible the establishment of weed seedlings germinating on the plot in the spring. The fall-germinated cheatgrass plants on the unhoed plots were 8 inches tall and in head on May 10, when the late-winter- or early-spring-germinated cheatgrass on the fall-hoed plots was only 2 inches tall and still in a vegetative stage of development.

Table VI shows the per cent survival of bitterbrush seedlings and their heights on the variously treated plots at several dates during the first growing season. It will be noted here that heaviest mortality of newly emerged bitterbrush seedlings in early spring occurred in undisturbed cheatgrass. This supports the findings of the previous year in the first test described above.

By July, both average plant height and percentage survival in the fall- and spring-hoed plots were significantly greater than in the fall-hoed plots. Grasshoppers became a factor after July. Almost all the bitterbrush seedlings surviving through September were defoliated by that time, and doubtless this had some effect on growth rate during late summer. In spite of these accidents, the effect of treatment appears to be exhibited in survival percentages and plant heights shown for September.

Table VI. Survival and growth of bitterbrush seedlings on cleared and partly cleared plots of various sizes in cheatgrass. 1951

Treatment and plot diameter	Number alive Apr. 12	Per cent survival of bitterbrush seedlings				Average height (inches)	
		Apr. 12	May 10	July 9	Sept. 13	July 9	Sept. 13
Undisturbed cheatgrass	11	100	27	18	9*	1.25	3.50*
Fall-hoed 1 foot	14	100	43	21	14	1.33	1.00
1½ feet	20	100	40	30	15	1.33	1.58
2½ feet	8	100	75	62	0**	1.40	....
4 feet	13	100	38	31	15	1.12	1.50
Fall- and spring-hoed							
1 foot	29	100	55	55	38	1.94	2.95
1½ feet	19	100	47	47	37	2.06	4.14
2½ feet	10	100	60	40†	40	2.75	4.25
4 feet	15	100	67	67	67	2.85	3.46

*Single plant growing at edge of bare area.
**Mortality between July and September obviously caused by defoliation by grasshoppers.
†Mortality between May and July caused by moth larvae in May.

The anomalous September height shown in Table VI for the bitterbrush in the undisturbed plot warrants special mention. This is the height of the single surviving plant of that treatment. It grew at the edge of a small area about 2 feet across in which for some undetermined cause cheatgrass and other weeds failed to grow in 1951, but where weeds grew in both 1950 and 1952. It seems reasonable to explain the excellent growth of this plant by the similarity of its natural situation to that created artificially by removing weeds.

Associated with the 9 plots in each of the 5 sets just described were 4 other plots prepared and planted at the same time. These plots were scalped; *i.e.*, the surface 2-inch layer of soil and plant litter was scraped off. They were 1 foot, 1½ feet, 2½ feet, and 4 feet in diameter. The purpose of this trial was to test a manual method of weed removal on steep slopes, one that could be accomplished at the time of planting in the fall, thereby eliminating the need for subsequent weeding during the first growing season. The supposition, in selecting this method for testing, was that not only fall-germinated weeds, but dormant seeds—potential weeds—as well, would be removed from the seedbed, which does not happen when plots are merely hoed. The loose nature of the granitic soil, and the absence of perennials in the vegetation made the treatment easy to apply. That it was effective was indicated by weed counts in the spring of 1951. There was an average of 4.2 weeds, all spring-germinated, per square foot on the scalped plots, as compared to 14.0 fall-germinated weeds on the undisturbed plots previously mentioned and 34.8 spring-germinated weeds on those merely hoed in the fall.

Survival and growth of bitterbrush seedlings on the scalped plots are shown in Table VII. Plant heights and survival percentages were comparable to those shown for the fall- and spring-hoed plots in Table VI. The similarity in results reflects the similarity in weediness of the plots under the two treatments—that is, few late-starting weeds or no weeds at all. As with the fall- and spring-hoed plots, an advantage was shown by the larger size of scalped plot. Tables VI and VII suggest that

for best growth and survival of bitterbrush seedlings on this cheatgrass-covered site, the minimum diameter of cleared plots might be about 2½ feet, but the number of seedlings in the plots was too small to demonstrate this statistically.

TABLE VII. Survival and height of bitterbrush on five scalped plots of each of four sizes. 1951

Diameter of scalped areas	Number alive Apr. 12	Per cent survival of bitterbrush seedlings				Average height (inches)	
		Apr. 12	May 10	July 9	Sept. 13	July 9	Sept. 13
1 foot	16	100	56	56	31	1.50	2.60
1½ feet	17	100	76	76	41	1.54	3.00
2½ feet	15	100	67	67	53	2.50	4.38
4 feet	20	100	70	70	50*	2.07	4.05

*Three of four seedlings lost between July and September were presumed to have died as a result of setback caused by moth larvae in May.

YEAR DIFFERENCES

The inhibitory effect of annual weeds on establishment of seedling bitterbrush, though consistent, varies from year to year in degree or intensity and in date at which it becomes apparent. Illustrative of this are results of a comparison of planting methods run for two years at Dement Ranch on the South Fork of the Boise River. Cheatgrass dominated this site, but filaree (*Erodium cicutarium* (L.) L'Her.), another winter annual, was also abundant in the cover.

Four seedbed preparation and planting treatments were applied to one plot in each of 20 rows of plots on a south-facing slope in November, 1951, and repeated in 10 rows of plots in October, 1952. The plots consisted of: (1) scalps 3½ feet square, (2) scalps 2½ feet square, (3) scalps 1½ feet square, and (4) undisturbed annual cover. Ten bitterbrush seeds were planted singly within a 9-inch diameter circle in the central part of each plot.

In 1952, there was an average of less than one annual per square foot on plots scalped the previous fall as compared to 143 on undisturbed plots. The 1953 weed number averages for the 1952 plot series were 2 and 114, respectively.

Emergence of bitterbrush occurred in late March and early April both years and seedlings were counted at irregular intervals during the spring and early summer of their first growing season. Each time counts were made, the apparent causes of mortality that had occurred since the previous date of observation were recorded. Insect and frost damage were obvious, as was damping-off. Where the leaves had withered and burned, indicating insufficient soil moisture, "drought" was the assigned factor. In a few instances, it was impossible to deduce a cause of mortality.

Frost heaving, damping-off, and insect larvae caused considerable early mortality, but no mortality occurring before April 22 in 1952 and before April 20 in 1953 could be attributed to insufficient soil moisture. In order to show more clearly the degree of drought mortality associated with the different plot treatments, the breakdown of causes of mortality in Table VIII includes only that occurring after those dates and before the time each year that grasshopper and rodent depredations obscured the differences in treatment effect.

TABLE VIII. Causes of mortality of bitterbrush seedlings occurring after April 22, 1952 and April 20, 1953, but before rodents or grasshoppers exerted their effect, in cleared plots of various sizes

Width of scalped plots	Original number (100%)	Per cent bitterbrush dying, by cause				Per cent survival
		Drought	Damping-off	Insect	Unknown	
1951 Series - 1951 Data						
Plots not cleared	74	87.8	....	3.7	1.4	8.1
1½ feet	66	6.1	....	1.5	3.0	89.4
2½ feet	96	....	....	4.2	3.1	93.8
3½ feet	34	....	....	5.9	2.9	91.2
1952 Series - 1953 Data						
Plots not cleared	68	38.2	13.2	1.5	7.4	39.7
1½ feet	41	9.8	17.1	...	4.9	68.3
2½ feet	26	11.5	11.5	...	...	76.9
3½ feet	24	....	4.2	4.2	...	91.7

The ability of annuals to suppress establishment of bitterbrush seedlings and the advantage of a cleared seedbed were again demonstrated, but there was a difference in season of occurrence of mortality in the two years that is not shown by the table. Heavy mortality of seedlings because of "drought" in the weedy plots occurred in early spring in 1952. Such "drought" did not occur until midsummer in 1953, the difference, no doubt, being associated with the dissimilarity of spring weather in those years. The progressive die-off of bitterbrush is plotted for each year in Figure 2.

April, May, and June, 1952, were much drier and warmer than the same period 1953. Figure 2 shows the precipitation pattern of the early part of the growing season for both years at Arrowrock Dam, the nearest weather recording station (U. S. Weather Bureau data 1952 and 1953). Arrowrock Dam, 12 miles northwest of the study area, is in the same general foothill region as the Dement Ranch, and the two sites are essentially the same in elevation and topographic situation. Mean monthly temperatures for April, May, and June, 1952, were from 4.4° to 5.7° F. higher than for

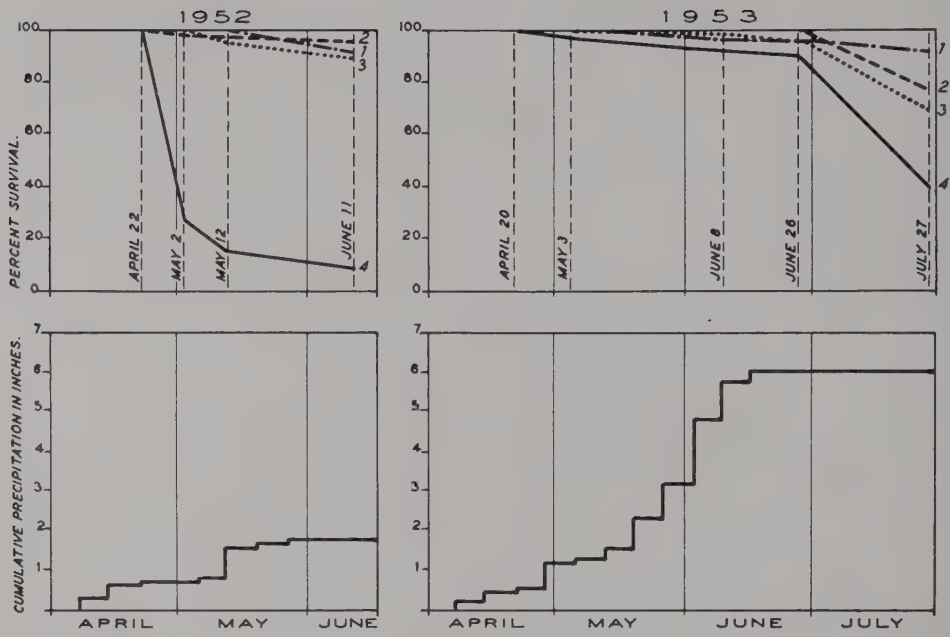

FIG. 2. Per cent survival during first growing season of bitterbrush seedlings alive April 22, 1952, and April 20, 1953, at Dement Ranch, and cumulative precipitation at Arrowrock Dam by 7-day periods (U. S. Weather Bureau records). Plot treatments are: (1) scalps 3½ feet across, (2) scalps 2½ feet across, (3) scalps 1½ feet across, and (4) undisturbed annual weed cover.

the corresponding months in 1953, and evaporation from a free-water surface in May and June was 2.19 inches more in 1952 than in 1953 at Arrowrock Dam. Thus, the spring of 1953 had more precipitation, a more favorable distribution of precipitation, lower temperatures, and resultingly lower evaporation than the spring of 1952.

The weather difference was reflected on the study area by different vegetational aspects in the two springs. By the first week in June, 1952, cheatgrass and filaree had matured and were dry. In 1953, these species grew more luxuriantly and did not attain the same stage of maturity until about 3 weeks later. The broad-leaved annual fiddleneck (*Amsinckia* sp.), which had been a very minor constitutent of the cover in 1952, was abundant in 1953, suggesting a supply of available moisture that year beyond the requirement of the usual cheatgrass-filaree complex.

Heaviest loss of bitterbrush seedlings in 1952 on the weedy plots occurred during a 3-week period in April and May, when there were only two days having measurable precipitation, the total of which was 0.10 inch. This sudden high mortality, nearly all apparently due to insufficient soil moisture and happening at a time when the roots of the newly emerged bitterbrush seedlings were still in the root zone of the annuals, compared with the total survival of bitterbrush through the same period on the scalps, points up the inefficiency of bitterbrush seedlings as competitors with winter annuals. In contrast to the results in 1952, there was negligible mortality from lack of moisture on the weedy plots until well into the summer of 1953, no doubt an effect of the frequent increments of rainfall and the lower temperatures throughout the spring season. However, even with the favorable moisture situation in 1953, the competitive effect of weeds on bitterbrush seedlings was apparent in May and June from the shorter stature of seedlings, narrower leaves, and earlier drying of cotyledons on the weedy plots than on the scalps. After the dry period started in mid-June, mortality was heavy on the weedy plots, not because of current competition with weeds, which were virtually all dead by that time, or died shortly afterward, but presumably because earlier competion had retarded the development of bitterbrush seedlings, leaving them unfit for survival through the summer drought.

SUMMARY

A series of studies was conducted between 1949 and 1953 to show the influence of annual weeds on

establishment, growth rate, and survival of artificially seeded bitterbrush on Idaho game winter ranges. A variety of aspects of the competitive effect of annuals was revealed.

Briefly, the results of the study indicated that:

1. In cheatgrass stands, few bitterbrush seedlings are able to survive the first summer. The competitive effect of cheatgrass generally becomes manifest early in the growing season, coinciding with its period of rapid growth.

2. Bitterbrush seedlings are better able to compete with broad-leaved, summer-annual weeds than with cheatgrass. The competitive effect of broad-leaved annuals becomes manifest later in the first growing season, coinciding again with their period of active growth.

3. Although broad-leaved weeds are less severe competition for seedling bitterbrush than is cheatgrass, their inhibiting influence results in stands of low-vigor bitterbrush plants that continue to die off for two or three years.

4. Fall-germinating cheatgrass, because of its advanced development at the time of bitterbrush germination, is a more severe competitor than spring-germinating cheatgrass.

5. The competitive effect of cheatgrass extends more than one foot toward the center from the edge of a cleared plot.

6. Bitterbrush seedlings that grow their first season in freedom from competing weeds are vigorous. Subsequent invasion of weeds results in only negligible or no mortality, but it causes a slowing up in the growth rate of bitterbrush.

7. Removal in the fall of a 2-inch layer of soil from the surface of a plot is an effective method of eliminating the crop of annual weeds the following year. The principle of this scalping is to remove weeds and weed seeds at the same time.

8. Severity of competition effects and the time of year they become noticeable vary from year to year. This variation is doubtless a function of the weather.

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CORRECTION

Correction for article on prairie continuum, Ecology **36**(4) : 558-566. 1955. The formula as given on p. 560 is incorrect, and should read as follows:

$$\frac{(1\times1) + (5\times2) + (8\times3) + (7\times4) + (0\times5)}{1+5+8+7+0} = \frac{63}{21} = 3.00 \times 100 = 300.$$

J. T. Curtis

POCKET GOPHERS AND SEEDLINGS OF RED FIR[1]

Ingles (1952), who studied *Thomomys monticola* on meadows of the Sierra Nevada, concluded that gophers did not reduce the value of land for domestic animals.

On the other hand, an exceptionally large population of gophers, such as that on the Hoopa range, is likely to intensify the effect of grazing by livestock and to contribute to deterioration of turf. The animals may undermine the sod, which then is killed when cattle step through it (Garlough 1937); remove surface vegetation from a radius of approximately eight inches of tunnel openings (Aldous 1951); and smother some plants by covering them with mounds (Moore and Reid 1951).

All these latter effects were to be seen when I first visited the Hoopa range on July 4, 1952. The pattern of old subterranean runways under surviving patches of turf was conspicuous because cattle in breaking through the tunnels had killed the grass, causing formation of erosion gullies; and intensive burrowing and mound-building by rodents in bare ground, which was no longer visited by cattle, prevented the return of fescue. In Oregon, Moore and Read (1951) noted that perennial grasses did not rejuvenate on grazed land until gophers had been excluded.

Because of destruction of turf by cattle and continuous plowing of ground by gophers, much of the Hoopa range was bare mineral soil—an ideal seed bed for conifers—when in 1951 red fir set the largest cone crop of recent years. This reproductive surge of unusual intensity was not a local phenomenon. In California, it occurred in the Sierra Nevada, Cascades, and Klamath Mountains; it was reported also in southern Oregon (Stein 1954).

As a result of the showers of seed which fell on the Hoopa range during the autumn and winter, innumerable seedlings sprouted the following spring (late June and early July) on snowdrifts, turf, and bare ground. At the time of my first visit to the region, all of those on the snow were doomed, and most of those on the turf were dying, having failed to penetrate the interlocking roots of grass; but ones on bare mineral soil were rooted and healthy. There was a tendency for them to be concentrated in clusters, which marked sites of disintegration of cones, and in small depressions and incipient gullies, into which seed had been swept by rain.

The die-off during the first summer was considerable. It was caused mainly by drought and heat, for seedlings of fir prefer light shade during the first year of their lives (U. S. Forest Service 1948: 59), and those on the Hoopa range were fully exposed to the sun. There was some loss, too, from insect clipping and the activities of cattle and gophers. Even so, in early August, fifteen milacre-quadrats selected at random on bare ground two hundred feet from trees and having a northwest exposure gave an average of 579,000 seedlings of red fir per acre.

Some two years later, in November 1954, a comparable count was made in the same area. It averaged 1,210 seedlings per acre. Mortality had been high. Nonetheless, the number of seedlings surviving three summers indicated that much of the range within three hundred feet of trees was fated to be transformed into forest.

In August of its first year, a typical healthy seedling had been 2¼ inches in length with a 6-inch root, which

An important summer range for cattle from the Hoopa Indian Reservation in northwestern California rises above the coniferous forests of the New and Trinity rivers. Known locally as "mountain prairie", it consists of long stretches of open country interspersed with stands of red fir (*Abies magnifica* Murr.). Climatic conditions are severe. In winter, the ridge, which is between 5,500 and 6,000 feet in elevation, is swept by freezing wind and blanketed by deep snow. In summer, the granitic soil suffers extreme desiccation.

Around the turn of the century, when Indians first pastured livestock on the New River-Trinity Divide, a solid turf of Idaho fescue (*Festuca idahoensis* Elmer) prevented encroachment of red fir. Then each year more cattle were driven up from Hoopa Valley than the range could support without damage. Although Idaho fescue can withstand heavy grazing and trampling, ultimately it succumbs to continued abuse (Dayton 1937). Today erosion gullies are common. Large areas of the range have lost all turf, and, except for scattered rosettes of pussytoes (*Antennaria*) and perennial forbs with deep or bulbous roots, the ground is bare.

Along with deterioration of the range, pocket gophers (*Thomomys monticola* Allen) appear to have increased markedly. Abundance of their mounds on semi-bare ground compared with scarcity in the few places where turf remains support this conclusion. Then too, increase of gophers on ranges depleted by overgrazing is a common phenomenon. In Texas, Buechner (1942) counted approximately eighteen times more mounds on overgrazed range than on land free of cattle. Garlough (1937) generalized that gophers which often are comparatively rare in old sod become numerous when heavy grazing replaces grass with secondary plants.

Although many kinds of rodents prosper on depleted grassland, different species are benefited for different reasons (Bond 1945). In the case of the pocket gopher, the most frequent explanation is that the bulbous and deep-rooted plants whch flourish when turf disappears are an important food—and more food means more animals.

Ecologists generally agree that even on ranges where gophers are numerous, overgrazing by livestock is the primary cause for deterioration of the vegetative cover (Ellison 1946). Selective feeding by cattle or sheep replaces palatable plants with less desirable ones, trampling packs the soil and injures and breaks up the turf, and trail-formation leads to gully erosion.

In contrast to the deleterious effect of excessive numbers of livestock, gophers by themselves are not always harmful and may be beneficial. When livestock was excluded from a study plot in the subalpine grassland of Utah, Ellison and Aldous (1952) observed that grasses and sedges multiplied most rapidly if gophers were not removed. The improved production of forage was attributed to the fact that soil which for many years had been compacted by the trampling of sheep was cultivated and aerated by tunneling and mound-building of rodents.

[1] This study was made in cooperation with the California Forest and Range Experiment Station of the United States Forest Service. It was suggested by Ranger Wesley E. Hotelling of the Six Rivers National Forest.

was only an inch deeper than the layer of dry soil. Growth during the succeeding two years was slow. A typical survivor in its third year was stunted—only 2½ inches high—but the stubby trunk had five branches and was so deeply rooted that it could not be pulled from the soil.

Counts made in 1954 in various habitats of the region showed that surviving seedlings were abundant only on bare ground from which gophers had removed all other vegetation. They were moderately common on areas overgrown with bracken (*Pteridium*); rare in manzanita (*Arctostaphylos*) brushfields and on semi-bare ground where bulbous and deep-rooted plants still attracted gophers; and practically absent on turf and in the mature forest of red fir. In 1952, an average of 448,000 seedlings per acre had been recorded in the forest; hence, mortality in that habitat had been greater than in any other. Oosting and Billings (1943) state that seedlings are not likely to live longer than a year or two in the shade of trees.

Cattle did not eat seedlings. Their trampling killed appreciable numbers only during the first summer. Thereafter the young plants were protected by their deep roots. This was strikingly demonstrated by the fact that seedlings were very numerous on the trampled ground surrounding a pond where cattle congregated to drink and wallow. As on the Devil's Table of central Washington (Rummell 1951), livestock actually contributed to the spread of conifers by checking the growth of grass.

Gophers were quite destructive to seedlings on the Hoopa range. Large numbers of young plants survived only on barren areas which the rodents did not visit in their search for food. On semi-bare ground, excessive activity by the animals caused nearly complete disappearance of seedlings. Some were smothered by mounds and earth cores, and others, which grew within a few inches of burrow openings, were eaten. But the greatest loss resulted from exposure of the roots of seedlings to air by continuous tunnel-building. In the Ochoca National Forest of Oregon, Moore (1943) believed that gophers were responsible, at least indirectly, for lack of reproduction of pine in some clearings. Stein (1954) listed them as one of the causes of mortality of red fir seedlings in the Rogue River National Forest.

When the total effect of gophers on red fir seedlings of the Hoopa range is considered, the role of the animals in creating seed beds perhaps should be emphasized more than destruction of young plants. Cattle started the depletion of vegetation, but gophers by eating grasses and herbs, burrowing under turf, and plowing up ground accelerated the trend and made conditions favorable for advance of conifers. If the turf had not been replaced by bare mineral soil, a large catch of red fir seedlings would not have occurred in 1952 in spite of the abundance of seed. There is a parallel in the Wenas region of Washington, where Larrison (1942) recorded that pine seedlings sprouted and thrived in dirt thrown up by gophers on otherwise unfavorable terrain.

At the present time, deterioration of the Hoopa range may have progressed beyond the stage at which restoration of original conditions is feasible, for seedlings of red fir are established in sufficient numbers to indicate that within a century much of the former grassland will be forested. From an economic standpoint, the most profitable use of the land might be to grow Christmas trees; but if restoration of the range is desired, then corrective measures are needed. Only light grazing by livestock should be permitted, salt blocks should be used to keep cattle on the wet meadows below the ridge, bare areas should be seeded with grass, and gophers should be reduced in numbers. Moore and Reid (1951) found that removal of gophers from overgrazed meadows improved the condition of the range; but as Kalmbach (1948) warned, rodent control without provision for reseeding and livestock reduction is a temporary palliative.

Control of gophers is difficult, arduous, and time-consuming, and, because of rapid reinvasion of animals from adjacent areas, can never be permanent The most effective poison is Compound 1080 (Miller 1953). It should be placed on suitable baits on main runways of the animals (U. S. Fish & Wildlife Service 1952). Because deaths occur in the burrows, there is little danger of secondary poisoning of other wildlife (Eadie 1954: 188).

Along with attempts at artificial control of gophers, predators should be encouraged. In 1952, I examined sixteen scats of coyotes from the vicinity of the Hoopa range. All contained hairs of gophers. Yet a trapper of the United States Fish and Wildlife Service takes coyotes from the area every summer.

Summary

A high ridge between the New and Trinity rivers in northwestern California originally was covered with a turf of Idaho fescue (*Festuca idahoensis* Elmer) which prevented the spread of conifers. Around the turn of the century, Indians from the Hoopa Reservation began to pasture large numbers of cattle on this mountain rangeland. Overgrazing by livestock resulted in gradual destruction of the turf and multiplication of deep-rooted and bulbous plants. Then pocket gophers (*Thomomys monticola* Allen), responding to a new supply of food, increased in numbers. Their burrowing accelerated deterioration of the range.

Removal of vegetation and churning of ground by gophers produced an ideal seed bed for conifers. In 1951, red fir (*Abies magnifica* Murr.) set a bumper crop of cones. In the following spring, enormous numbers of seedlings sprouted. Mortality was high. After two years, abundant survivors were found only on bare ground not visited by the rodents. In brushfields and forest, young trees disappeared because of shade and competition from other plants.

After two years, seedlings that had survived on bare ground were sufficiently numerous to indicate that much of the range is destined to become forest. A reversal of this present trend in ecological succession will require reduction in numbers of livestock and gophers, and seeding of bare areas with grass.

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LOW TEMPERATURE DIFFERENTIALS IN ONE FOREST DRAINAGE

A knowledge of the distribution and variability of low temperatures through a ponderosa pine (*Pinus ponderosa* Laws.) forest is often of concern to foresters in judging how effective a period of cold weather has been in killing destructive bark beetles. That low temperatures can be fatal to overwintering broods of the western pine beetle (*Dendroctonus brevicomis* Lec.) was first discovered in 1924 on an area near Bend, Oregon, by A. J. Jaenicke of the Forest Service. Since then, various aspects of the effect of low temperatures on beetle broods have been studied in the laboratory and in the field. Miller (1931) determined the high and low temperatures fatal to this bark beetle in the laboratory. Yuill (1941), also working in the laboratory, studied its cold hardiness as affected by the season of the year, the suddenness of temperature change, and the duration of critical low temperatures. Beal (1934) determined the modifying effect of bark of different thicknesses in protecting broods during periods of low temperature. Keen and Furniss (1937) determined the average precentage of brood mortality that can be expected from different low winter temperatures experienced in the ponderosa pine forests of eastern Oregon and northeastern California; for temperatures, they used weather records available from standard weather stations near the forested areas. The need to use such records raised questions as to how well temperature readings taken at standard weather stations, usually in towns near the forest, actually represented temperatures prevailing under forest conditions.

To answer these questions, an experiment was designed in 1936, and the Ochoco Creek drainage of the Ochoco National Forest in east central Oregon (Fig. 1) was selected for the experiment. Near the center of this drainage, in a narrow valley, was a year-long weather station maintained at the Ochoco Ranger Station of the Forest Service. Another year-long weather station, maintained at the town of Prineville, some 27 miles to the west in a broad, open valley, gave an additional comparison. The study area comprised a ponderosa pine forest of 88,000 acres in rough, mountainous terrain ranging in elevation from 3,500 to 6,500 feet.

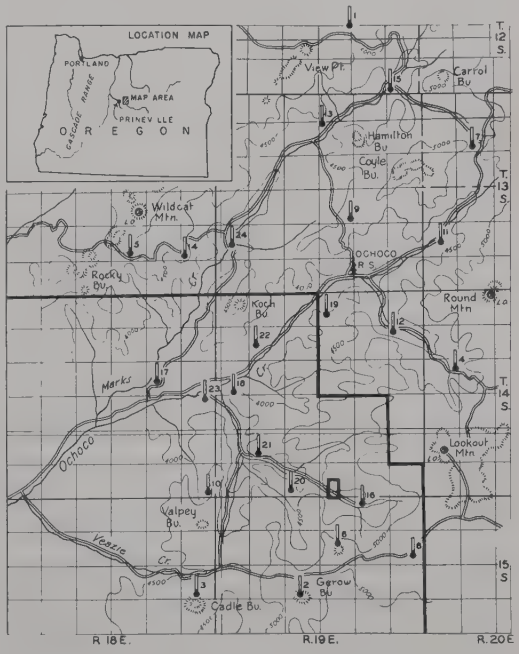

Fig. 1. Location of low-temperature stations, Ochoco Creek drainage, Ochoco National Forest, Oregon.

The experiment was designed for an analysis of variance (Snedecor 1934) in which were tested: 4 exposures —valleys, ridge-tops, north slopes, and south slopes; 3 elevation zones—low, medium, and high; 3 heights on trees—10 feet, 40 feet, and 70 feet; and 2 sides of the trees—north and south. In order to increase accuracy, two replications of the experiment were provided. This required the placing of 144 minimum-recording thermom-

eters—6 thermometers per tree on 24 trees—in the forest. Two additional thermometers were established on a tree at the base weather station at Ochoco Ranger Station.

The test area was first stratified by valley, north and south slopes, and ridges, and by 3 elevational zones. Then, after indicating on a map all possible locations within the stratified zones where section lines crossed roads under the conditions desired, these locations were randomized for the final selection of the 24 temperature stations.

From October 8 to 12, 1936, W. J. Buckhorn and the writer set up 146 thermometers in the field. Buckhorn climbed the trees and placed standard Weather Bureau minimum-recording thermometers on the north and south sides of trees at 10 feet, 40 feet, and 70 feet above the ground. The north and south sides of trees were determined by compass from the ground, and each thermometer was placed on an unshielded bracket nailed to the tree and leveled with a spirit level.

On November 2, 1936, the first spell of cold weather occurred. Temperatures dropped to +5° F. at Ochoco Ranger Station, and to +8° F. at Prineville. The temperature stations were visited November 5 to 7, trees were again climbed by Buckhorn, one complete set of readings was taken (Table I), and the thermometers were reset. The night of November 2 had clear, still air; this caused a typical temperature inversion, with the coldest air settling in the valleys and warmer air up the slopes.

During the night of January 8, 1937, a second cold spell occurred. This time, temperatures dropped to the extreme low of —36° F. at one test station on the area, with a minimum of —27° at Ochoco Ranger Station, and —24° at Prineville. This also occurred during clear, still atmospheric conditions. From January 9 to 14, 1937, W. J. Buckhorn and R. L. Furniss skiied through the study area, climbed the trees during weather of 15° below zero, and took a second set of readings (Table II). The ther-

TABLE I. Minimum temperatures in a ponderosa pine forest. Ochoco Creek Drainage, east-central Oregon, November 2, 1936

Base Station: Ochoco Ranger Station—Valley, elev. 3,980′ ..... 5.0 F.

Standard Weather Station: Prineville, Oregon—Valley, elev. 2,867′ ..... 8.0 F.

Zone and elevation (feet)	Aspect	Position on tree						Average temperature
		Low 10 ft.		Middle 40 ft.		High 70 ft.		
		N	S	N	S	N	S	
High Zone				Degrees Fahrenheit				
5,740.....	Ridge	12	13	13	14	13	13	13.0
5,620.....	Ridge	9	9	9	10	9	10	9.3
4,820.....	North	16	16	17	17	17	17	16.6
5,180.....	North	14	14	14	14	14	14	14.0
4,960.....	South	13	13	15	16	16	16	14.8
5,010.....	South	14	14	15	15	16	16	15.0
4,980.....	Valley	7	7	10	9	10	10	8.8
5,540.....	Valley	8	8	10	9	11	11	9.5
Average.....	.....	11.6	11.8	12.9	13.0	13.2	13.4	12.6
Middle Zone								
4,700.....	Ridge	15	15	17	17	17	17	16.3
4,210.....	Ridge	6	7	10	9	10	(10)*	8.7
4,360.....	North	6	7	(9)	9	9	9	8.2
4,400.....	North	8	9	9	10	10	10	9.3
4,460.....	South	12	12	13	14	14	15	13.3
4,610.....	South	12	12	13	14	14	15	13.3
4,380.....	Valley	−1	−2	0	0	2	2	0.2
4,500.....	Valley	7	7	8	8	9	9	8.0
Average.....	.....	8.1	8.4	9.9	10.1	10.6	10.9	9.7
Low Zone								
3,680.....	Ridge	4	5	6	6	8	8	6.2
3,950.....	Ridge	9	9	10	10	10	10	9.7
4,050.....	North	9	10	10	10	10	10	9.8
4,100.....	North	9	10	11	11	11	11	10.5
3,960.....	South	5	5	6	6	7	7	6.0
3,980.....	South	9	8	9	10	9	9	9.0
3,610.....	Valley	1	1	2	1	3	2	1.7
4,020.....	Valley	1	1	2	2	3	2	1.8
Average.....	.....	5.9	6.1	7.0	7.0	7.6	7.4	6.8
Average of all.	.....	8.5	8.7	9.9	10.0	10.5	10.5	9.7

*( )=Temperature estimated.

TABLE II. Minimum temperatures in a ponderosa pine forest. Ochoco Creek Drainage, east-central Oregon, January 8, 1937

Base Station: Ochoco Ranger Station—Valley, elev. 3,980′ .....—27° F.

Standard Weather Station: Prineville, Oregon—Valley, elev. 2,867′ .....—24° F.

Zone and elevation (feet)	Aspect	Position on tree						Average temperature
		Low 10 ft.		Middle 40 ft.		High 70 ft.		
		N	S	N	S	N	S	
High Zone				Degrees Fahrenheit				
5,740.....	Ridge	(−18)*	−17	(−18)	(−17)	(−18)	(−17)	−17.5
5,620.....	Ridge	−15	−15	−15	−14	(−14)	−14	−14.5
4,820.....	North	−15	−15	−15	−16	−15	−15	−15.2
5,180.....	North	−16	−15	−16	−16	−16	−16	−15.8
4,960.....	South	−15	−16	−15	−14	−16	−15	−15.2
5,010.....	South	−16	−16	−15	−16	−14	−15	−15.3
4,980.....	Valley	−21	−21	−19	−21	−19	−19	−20.0
5,540.....	Valley	−17	−17	−16	−16	−15	−16	−16.2
Average.....	.....	−16.6	−16.5	−16.1	−16.2	−15.9	−15.9	−16.2
Middle Zone								
4,700.....	Ridge	−16	−16	−16	−16	−15	−16	−15.8
4,210.....	Ridge	−26	−24	−22	−22	−23	−22	−23.2
4,360.....	North	−23	−21	−22	−21	−21	−21	−21.5
4,400.....	North	(−22)	−22	−22	−21	−21	−22	−21.7
4,460.....	South	−27	−27	−26	−26	−25	−26	−26.2
4,610.....	South	−18	−17	−19	−18	−19	−17	−18.0
4,380.....	Valley	−31	−32	−29	−29	−27	(−27)	−29.2
4,500.....	Valley	−23	−23	−22	−22	−21	−21	−22.0
Average.....	.....	−23.2	−22.7	−22.2	−21.9	−21.5	−21.5	−22.2
Low Zone								
3,680.....	Ridge	−28	−27	−27	−27	−25	−23	−26.2
3,950.....	Ridge	−24	−23	−23	−23	−23	−23	−23.2
4,050.....	North	−25	−24	−22	−23	−23	−23	−23.3
4,100.....	North	−22	−21	−22	−23	−20	−20	−21.4
3,960.....	South	−26	−27	−28	−27	−27	−26	−26.8
3,980.....	South	−24	−23	−23	−24	−23	−23	−21.4
3,610.....	Valley	−32	(−32)	−31	−31	−29	−31	−32.7
4,020.....	Valley	−36	−35	−33	−33	−31	−32	−33.3
Average.....	.....	−27.1	−26.5	−26.2	−26.4	−25.1	−25.1	−26.1
Average of all.	.....	−22.3	−21.9	−21.5	−21.5	−20.8	−20.8	−21.5

*( )=Temperature estimated.

mometers were taken down during the next spring and, in spite of winter weather, falling limbs, icicles, tree climbing, and other hazards, not a single thermometer had been broken.

Temperature Differences

The total spread in temperature between all 144 thermometers was 19° F. on November 2, and 22° F. on January 8. The temperature differences recorded (Table III) show that: (1) This forested area was about 5 degrees warmer than the valley where the base weather station was located, and about 2 degrees warmer than the standard weather station at Prineville, 27 miles away. (2) Temperatures increased from low to high elevations. (3) Ridges and slopes were warmer than valleys. No significant difference in temperature occurred between north and south slopes, and ridges. (4) It was warmer high in the trees than near the ground. (5) There was practically no difference in temperature according to side of tree.

In order to determine the source of variation and test the significance of differences, the data were analyzed by the variance method. These analyses showed highly significant differences in temperature by the three elevational zones, by aspect, and by height on tree, but no significant difference by side of tree. There was also a significant difference by location of paired stations on the same aspect and at the same elevational zone on January 8, but no difference between these paired stations on November 2 when the low temperatures were milder. The analyses show significant interactions between elevation and aspect, elevation and location, and aspect and location. These interactions mean simply that each temperature station had individual characteristics in respect to temperatures, owing to its location, which made it significantly different from others on the same slope and at the same general elevational level. The interaction of elevation and aspect indicates that temperature differences between various aspects, were modified by elevational level. For instance, there appears to have been more difference between slopes and valleys at low elevations than at high.

Because the study period was one of typical temperature inversion, the weather conditions favored large differentials in temperature, and so this study shows what large differences may occur, rather than the minimum difference to be expected.

In cold periods previously studied in eastern Oregon (Keen and Furniss 1937) and in northeastern California (Miller 1933), quite different conditions prevailed. In Oregon, during the cold period from December 7 to 17, 1932, "a strong wind blew more or less constantly, resulting in a thorough agitation of the air so that similar temperatures prevailed over wide areas" (Keen and Furniss 1937). Thus, under conditions of a freeze when great polar air masses sweep across the country, the differentials between forest temperatures and nearby standard weather stations are likely to be negligible.

For the forest entomologist, the important findings of this study were that during two cold periods forest temperatures were indicated fairly well by readings taken at the base station in the forested area, and by a standard weather station in a town some 27 miles away. If the average difference in minimum temperatures had been predetermined between the standard weather station and nearby forest stations, the forest temperatures could have been estimated with a reasonable degree of confidence—at last sufficiently closely to have estimated the degree of western pine beetle mortality.

This study also indicated that during the cold periods studied high elevations were up to 10 degrees warmer than low elevations, slopes were up to 7 degrees warmer than valleys, and at 70 feet up the tree trunks it was some 2 degrees warmer than at the 10-foot level. It is reasonable to expect that smaller differences might have occurred if the cold periods had been due to invasion of polar air masses rather than to heat loss through radiation and temperature-inversion conditions.

Table III. Temperature differences by location of test thermometers in ponderosa pine forest, eastern Oregon

Location	November 2, 1936 Average difference from —		January 8, 1937 Average difference from —	
	Weather base sta.* (Ochoco Ranger Sta.)	General average of study area†	Weather base sta.* (Ochoco Ranger Sta.)	General average of study area†
	°F.			
Elevation Zone				
High, 3,500-4,000...	+7.6	+2.9	+10.8	+5.3
Middle, 4,100-5,000.	+4.7	0.0	+4.8	−0.7
Low, 5,000+.....	+1.8	−2.9	+0.9	−4.6
Aspect				
Ridge.....	+5.5	+0.8	+6.9	+1.4
North Slope.....	+6.4	+1.7	+7.2	+1.7
South Slope.....	+6.9	+2.2	+6.2	+0.7
Valley.....	10.0	−4.7	+1.7	−3.8
Height on Tree				
70 feet.....	+5.5	+0.8	+6.2	+0.7
40 feet.....	+5.0	+0.3	+5.5	0.0
10 feet.....	+3.6	−1.1	+4.9	−0.6
Side of Tree				
North.....	+4.65	−0.05	+5.4	−0.1
South.....	+4.78	+0.08	+5.6	+0.1
General Average.....	+4.7	0.0	+5.5	0.0
Standard error.....	.....	±0.14	.....	±0.17

*Minimum temperatures at Ochoco Ranger Station were: Nov. 2, 1936, +8° F.; Jan. 8, 1937, −24° F. At town of Prineville: 5° F. and −27° F.
†General average was 9.7° F. on Nov. 2, and −21.5° F. on Jan. 8.

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[1] The California Forest and Range Experiment Station is maintained at Berkeley, California in cooperation with the University of California.

ARE CORALS REALLY HERBIVORES?

Having recently returned from a ten weeks' stay on an atoll (Kapingamarangi, Caroline Islands) where I had been a member of one of the Pacific Science Board's Atoll Research Teams, it was with particular interest that I read the recent paper of Odum and Odum (1955). That paper is one of the few which has attempted to discuss in quantitative terms the bioeconomy of coral reefs. The conclusion of these authors that the reef is a true climax community does not conflict with existing knowledge of other reefs. The calculation that the efficiency of primary production is about 6 per cent with a total production of 74,000 lbs./acre/year and an annual turnover of 12.5 times of the existing biomass gives an impression of the unusually high production and turnover evidently normal for coral reefs.

An extremely interesting facet of their study was the development of biomass pyramids for the reef as a whole from quadrat data on several individual parts of the reef. However, the inclusion of the corals as herbivores in these pyramids still seems open to question. Inferences were drawn from their own observations on corals and the associated zooxanthellae and filamentous algae that the corals are best considered herbivores. They also draw the same inference from the studies of "previous authors reviewed in" Kawaguti (1937) and Yonge (1930). In Kawaguti's papers no mention seems to be made of the role of the algae in the nutrition of the coral, nor is previous work reviewed, while Yonge (1930) states that the significance of the algae will be discussed in a later paper and that corals are carnivores, although numerous references are made to other studies whose conclusions differ from this.

It is well established that corals are capable of catching and digesting zooplankton, and the work of Yonge (1930), including data from species of forty genera of corals, certainly leaves little reason to doubt this. Yonge's study revealed many specializations of corals for the purpose of handling animal food, including the development of ciliary currents for food gathering and the emission of mesenterial filaments to grasp food, especially in forms with reduced tentacles. His study, moreover, shows that vegetable matter is invariably refused as food. A later paper, Yonge and Nicholls (1931) shows from numerous experiments that there is no evidence of digestion of zooxanthellae or of transference of material from the algae to the coral and that the algae are not necessary for initial growth and budding of newly settled colonies. Further, it is well accepted that the period of greatest feeding activity of corals is during the night hours and that only a relatively few corals are active during the daylight. The feeding period of corals, the dark hours, agrees with the normal period of maximal zooplankton abundance. In 1940, Yonge reviewed the work at the Great Barrier Reef carried on by him and his colleagues, as well as that of numerous other authors, and concluded (p. 384) that "Corals are specialized carnivores feeding on zooplankton for the capture and digestion of which they are highly specialized," and that "The zooxanthellae play no part in the nutrition of corals." It should be pointed out that "zooxanthellae" as used by Yonge, physiologically, include the skeleton-inhabiting filamentous algae as well as the zooxanthellae.

We are thus faced with a question concerning the trophic position of the corals in a biomass pyramid. If we place the corals at the top, as carnivores, then the Odums' pyramids cease to fit ecological theory. This would suggest that the corals, to support their mass, must be obtaining their nourishment from a source outside of the measured reef community.

With the above facts in mind, and using only the data given by the Odums for night samples of plankton in their study area, one finds that the average loss on ignition in the samples from the ocean, the algal-coral ridge and the zone of large heads is .0042, .0315 and .0263 gm/m^3, respectively. The Odums also give data on the percentage of plant material in these samples. If the ignition data are recalculated to represent only the animal fraction, since this is the only part usable by corals according to Yonge and others, they are .0039, .0204 and .0254. These results seem very difficult to explain since there appears to be a continuous addition of animal matter as the water crossed the reef at night, rather than the decrease which one might predict on the assumption that the corals are removing animals or animal matter during this period. The Odums' data then seem paradoxically to contradict the accepted fact that corals are zooplankton feeders. It may be, however, if one could measure rates of removal of "plankton" by corals from water as it crosses a reef, as well as rates of addition of "plankton" from the reef to that water, that the balance of these two processes would be such that there is a net addition of animal matter to the water as it crosses the reef. If this is so, it may be that the rates are high enough so that actually the corals do receive enough animal food to support themselves.

If we further examine the data on plankton supplied in the Odums' paper we discover that a single sample, that taken from water crossing the coral-algal ridge on July 17 at noon, has a very high organic matter content. The inclusion of this sample gives an average value for loss on ignition of .064 gm/m^3, whereas the exclusion of this sample would give an average of .028. This would markedly affect the curve shown in their Figure 11 (p. 313) but would not change the conclusion that there is an over-all loss by the reef to the lagoon. However, it might be noted that the data for the whole curve are based on a very small number of samples and that the datum for station E (a critical end-station) is from a single sample. Moreover, if we compare the values for day and night plankton, excluding the unusual large sample referred to above, we find there is little difference between the two sets of data, while if we include the large sample we find that the daytime plankton is much greater than the night plankton. This, again, is an unexpected result.

It appears, then, that the question, *"What is the relationship of algae to corals?"*, is more poignant than ever. The Odums' data seem to place the corals as herbivores, deriving nourishment from their associated algae, while the studies of Yonge and his colleagues on the Great Barrier Reef interpret corals as carnivores. If conclusions must be drawn, it seems that errors of fact or interpretation must be involved in these two opposing views.

The study of the Odums is a significant contribution to the subject of reef ecology. Certainly they are to be congratulated for having achieved so much under circumstances of limited time and limited facilities. While they have explored many parts of this complex community and provided us with the first attempt at a "balance sheet" for a coral reef, the central problem seems to remain unchanged. The Odums do not seem to have produced proof that corals are not carnivores, and they apparently recognize this themselves. Throughout their work they are critical of their own methods and are careful to point out deficiencies in their data and techniques and the

sweeping nature of the generalizations they have drawn. We are regrettably left with the necessity of admitting that the trophic relations of reef corals are still in doubt. Modern techniques utilizing radio-isotopes might be applied to this problem, and these, I believe, could answer the question clearly. No matter what the trophic position of corals in the biomass pyramids of reef communities, the Odums' work will remain as an outstanding example of pioneering in a difficult area of marine biology.

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CORALS AS PRODUCERS, HERBIVORES, CARNIVORES, AND POSSIBLY DECOMPOSERS

We are grateful to Cadet Hand for focusing discussion on the role of corals in ecosystems although his comment somewhat misrepresents the view given in the Eniwetok paper (Odum and Odum, Ecol. Monogr., **25**: 291-320. 1955). Our viewpoint was summarized on page 305: "the animal part of the coral is partly divided in trophic classification between two trophic levels, herbivores and carnivores" and again on page 310: "The single coral is first a producer, to a lesser extent (in many cases) an herbivore and somewhat of a carnivore." We suggest on page 299 that corals probably must obtain some food and especially critical nitrogen from plankton. Thus, we are in no way denying the well known observation that corals do ingest plankton. Perhaps the difficulty is mostly a matter of interpretation. To many, a "coral" means only the tissue in the colony especially adapted for carnivorous life; we are considering the entire coral colony as a unit in the ecosystem. The colony obviously contains tissue which is not carnivorous.

Actually, there are no data applicable to field conditions to indicate what percentage of coral metabolism should be assigned to various trophic levels. It is apparently the graphical picture of biomass in our Figure 10 that is misleading to readers. Without quantitative data to estimate the relative importance of the previously known plankton feeding and the symbiotic nutritive source, we made no attempt to split the animal part of the coral biomass in the graph, but placed the whole at the lower trophic level. We suggested that herbivore nutrition may be predominant for two reasons: (1) The amount of plant tissue in the coral colony was greater than the amount of animal tissue; (2) the quantity of oceanic plankton coming in from the desert ocean was far too small to support the large mass of corals. True, there was a large amount of "pseudoplankton" on the reef, but this consisted of mostly large particles of plant and animal material broken off from sessile organisms on the reef itself. While this pseudoplankton is important fish food, it is largely plant in content and presumably is not available to the delicate animal feeding apparatus of coral polyps.

In speaking of herbivore nutrition we are speaking of diffusible substances from symbiotic algae and not digestion of ingested, particulate algal products. As we have pointed out, and as Dr. Hand emphasizes, experimental evidence for such transfers is needed. Also, an urgently needed study is the plating out of bacteria in a vertical section from the inside of a massive coral to determine whether bacteria are numerous.

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THE FREQUENCY OF REDUCTION OF RAT POPULATIONS BY WEATHER

Recently ecologists have recognized that the limitation of populations by a particular factor must be discussed in quantitative terms. The question is not "does factor *A* limit the population" but rather "how frequently does factor *A* limit the population." Naturally the precision of measurement is an integral part of the problem, since one must establish a difference among estimates in order to claim a limitation. The form of limitation that usually becomes apparent is the occurrence of sufficiently severe conditions to reduce the population by an amount that can be detected by the method of measurement. Clearly a stationary population is limited by something but since many factors are acting, it is difficult to know the role of each. In contrast, if some factor changes obviously and if the population also changes, one strongly suspects that there is a causal relation, although experimental verification is desirable to establish the relation. The objective of this paper is to record an experience with rat (*Rattus norvegicus*) populations in Baltimore that provided some information on the question "How frequently is weather (principally rainfall) sufficiently severe to reduce the population by at least 20%."

Some general comments on limiting factors are desirable. A factor is considered to limit a population if a

change in the factor will result in a change in the population. Thus if factor A is increased the population will increase until some other factor comes into play. This view is essentially the naïve principle of the law of the minimum and it is recognized that natural events are not as simple as that law indicates. However, for the present purposes that formulation will suffice. If a factor is not limiting the population, then changes in it will not affect the population unless the changes are adequate to make the factor a limiting one. For example, suppose a population has just enough food but 10 times as much water as it needs. Radical increases or decreases (down to 0.1) in water supply will not change the population. In simple terms "water does not affect the population."

Observations on rat populations in Baltimore in the summer of 1955 indicate that severe weather affected the population. Since 1943 (Davis 1953) studies of rat populations have been conducted in a number of city blocks. The usual routine is to estimate the populations every 2 months by a method (Emlen *et al.* 1949) which has an error of about 10%. Thus a difference of 20% between 2 estimates usually indicates that the population has changed. During the decade of observations, weather conditions had no noticeable effect on the populations except in a few local spots. However, the severe drouth and rain in July and August of 1955 was correlated with a drastic decline in rat populations in many blocks. Table I shows the rainfall for July and August from 1945-55 inclusive. The means for July and for August 1817-1955 are also given. All data were taken from the published U. S. Weather Bureau records for Baltimore. Examination of the records from 1817 to 1954 shows that in only 2 years did July have less than 0.35 inches of rain. In no year was there 17 inches in August. In fact there are only 3 years with more than 10 inches and none with more than 14. Clearly 1955 was unusual.

TABLE I. Rainfall in Inches in July and August in Baltimore

Year	July	August
1945	9.68	2.48
1946	5.37	4.02
1947	4.92	3.74
1948	1.94	5.75
1949	3.24	2.82
1950	3.07	2.96
1951	3.11	0.77
1952	7.11	3.81
1953	4.54	3.25
1954	2.18	4.34
1955	0.35	17.69
From 1817 - 1955		
Mean	4.01	4.23
S.D.	2.24	2.73

The observations on rats can be analyzed by comparing the estimates in late June and early July (before the drouth or rain) with the estimates in September (after these events). Table II shows the percentage differences for various blocks in the past 4 years that were estimated in July (early), and in September and in November. No poisoning, trapping, or housing rehabilitation was done in these blocks. Similar data for previous years (1945-1951) are not given because only a few blocks fit the specifications. The differences from September to November are included to indicate whether the block was permanently changed or not. For 1952, 1953, and 1954 it is apparent that no regular decrease occurred in September. Some blocks increased and others decreased. In general in 1952 the blocks increased but in 1953 and 1954 the differences were usually within the error of measurement. For 1955 a decline in September is obvious. The populations returned to their former level in November.

TABLE II. Differences (in percent) between estimates in July and September and in September and November for various populations

Difference in percent	1952		1953		1954		1955	
	July-Sept.	Sept.-Nov.	July-Sept.	Sept.-Nov.	July-Sept.	Sept.-Nov.	July-Sept.	Sept.-Nov.
160-179	..	..	..	..	..	..	..	1
140-159	..	1	..	..	..	..	..	1
120-139	..	1		..	.	.	..	..
100-119	2	..	..	1	..	..	..	..
80-99	..	1	.	..	.	.	..	.
60-79	1	..	1	..	..	..	..	1
40-59	2	1	..	3	..	..	..	5
20-39	3	2	4	4	2	3	..	4
0-19	1	3	11	6	2	2	2	3
− 0-19	2	3	2	5	5	2	3	3
− 20-39	2	1	3	2	..	2	3	.
− 40-59	..	..	..	1	..	..	8	.
− 60-79	..	..	1	..	..	..	2	..
Blocks	13	13	22	22	9	9	18	18
Mean Diff.*	+34	+34	+ 5	+13	+ 3	+ 3	−34	+40

*Calculated from actual differences, not from midpoint of class.

These results are interpreted to indicate that the weather of July and August was sufficiently severe to reduce the populations. Obviously there is no control for an observation of this type. However, the absence of a summer decline in the 3 preceding years shows that a seasonal summer decline is not expected. Also the return in November 1955 of the populations shows that the blocks could maintain rats in terms of food and shelter.

Objective evidence of mortality of rats during July and August is unfortunately meager because no visits were made to these blocks between estimates of July and September. However, in September it was noticed that many burrow systems were washed in and destroyed, presumably by the torrents of rain (8 inches) that fell on August 12-13.

These histories permit us to consider the frequency of occurrence of weather that is sufficiently severe to reduce the population. We can analyze this in several phases. Suppose that the drouth of July was alone responsible for the decline. Since 3 out of 139 years were that dry, the probability is .0216 that drouth will reduce the population or, in simpler terms twice in 100 years we can expect a dry July to reduce the population. Obviously the population might be reduced by a July that was not quite as dry and had, say, one inch of rain. This would be 7 in 139 years or 0.05. Alternatively we can consider that only the heavy rain in August limited the population giving 1 out of 139 years or 0.0078. Possibly rain over 10 inches reduces the population giving $4/139 = 0.029$ as the probability. If both the dry July and the wet August were required then the probability is $(0.0216)\ (0.0078) = 0.00016848$ or twice in 10,000 years!

One could calculate these probabilities on the basis of a

normal curve using the standard deviations from Table I to indicate the probabilities of occurrence. However, the curve is badly skewed and thus is unsuitable for simple calculations.

This approach to the problem gives some idea of the frequency of weather conditions sufficiently severe to decrease the population. Clearly weather rarely can affect populations. The answer to the original question is "Weather affects rat populations less than 2-5 times in 100 years in this area."

Summary

The frequency of action of weather on rat (*Rattus norvegicus*) populations is considered. The numbers of rats in various blocks declined drastically in the summer of 1955 and returned to their former level by November. This change coincided with a drouth in July and a heavy rain in August. The frequency of such conditions is 3 and 1, respectively, in the 139 years of weather records for Baltimore. From these frequencies it is concluded that summer weather is sufficiently severe to reduce rat populations about 2-5 times in 100 years.

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THE PROVENDERING ROLE OF THE LARGER AQUATIC PLANTS

Rosine (1955) has contributed interestingly to knowledge of the limnological role of hydrophytes. He removed individual plants of *Chara delicatula, Potamogeton gramineus,* and *Polygonum natans* in a dip net from a Colorado alpine pond, enumerated the macrometazoans, and compared their occurrence qualtitatively and quantitatively on the three plant species. There are a few desiderata (which it may be unreasonable to wish for) including: (1) criteria defining so heterogeneous an assemblage of herbivores, carnivores, and omnivores; (2) comparative data on the invertebrates of *weedless* areas of the same or similar local ponds to throw light on the obligatory, facultative, or adventitious standing of the component inhabitants of the weed beds; (3) data on the same animals during the five or six months in winter when the weed beds die back. Rosine treats his quantitative data objectively and with admirable unpretentiousness; he found "only one (of seven counted) animal species was abundant enough to warrant individual treatment." (The maximum of this scud, *Hyalella azteca,* came in mid-June, was eight individuals per 100 square centimeters on *Polygonum*. . . .) I regret that my present ungrateful purpose is to dissent from an unwarranted premise of Rosine's introduction: "For some time evidence has been accumulating to show that relatively few aquatic herbivores and omnivores utilize the actual tissues of aquatic plants as food."

A controversy over the significance of the larger aquatics as food of invertebrates stems from Shelford's (1918) speculative dictum cited by Rosine as follows: "One could probably substitute glass structures of the same form and surface texture without greatly affecting the immediate food relations." Welch (1935) took a contrary view based on personal knowledge of a whole "array" of insects which eat water plants. He declared (in part): "It is now certain that the statement [Shelford's] is not well grounded; that these higher aquatic plants serve directly as food for a considerable array of animals, the quantities of the plants consumed sometimes being great. Moore (1915) showed that species of *Potamogeton* are extensively used in this way. Unpublished work done by the writer and his graduate students on Michigan lakes shows that none of these plants is exempt from direct feeding activities of animals; that not infrequently feeding activities are extensive enough virtually to devastate vegetation beds; that plants which seem to be exempt from attack are often only apparently so, *e.g.,* one of the common bulrushes, *Scirpus americanus;* and that all parts of these plants are potential forage. The aquatic feeders comprise a great array of invertebrates, the insects being a large component. . . ." If Dr. Welch's view of twenty years ago was justifiable it should now be even better documented by published information.

Merely noticing some American literature since Welch's résumé suffices to suggest the scope of unfolding knowledge of aquatic defoliators, miners, borers, etc. General papers with an avowed focus on the limnological role of hydrophytes have appeared since 1935: McGaha (1952); Berg (1949); Hoffman (1940c); and Frohne (1938), to mention only those dealing with insects which eat hydrophyte tissues. These particular authors have also published eleven supporting contributions classified primarily according to insect group. Furthermore, pertinent contributions are scattered through the memoirs on aquatic Diptera by Johannsen (1935, 1937a, 1937b). The plant host as a unifying criterion has appealed to some workers: Scotland (1940) on insects of *Lemna minor* and Berg (1949, etc.) on *Potamogeton* insects. Papers of the last type are especially praiseworthy ecologically when they do not single out for attention only a part of the fauna of a plant. Berg (1950a) studied certain chironomid larvae which bridge the gap between eaters of hydrophyte tissue and feeders on periphyton.

Now what particularly puzzles the writer and perhaps the reader of the present note is this: (1) is resurrection of Shelford's dictum based on refutation of the consensus of recent authors, or (2) has Rosine simply overlooked the scattered evidence showing that numerous aquatic insects utilize the tissues of water plants as food?

Summary

An old controversy over the limnological role of aquatics as food of invertebrates has been renewed by a recent paper (Rosine 1955) which claims "evidence has been accumulating that relatively few aquatic herbivores and omnivores utilize the actual tissues of aquatic plants as food."

The present author disagrees and cites some recent literature in support of Welch (1935) showing that, viewed either qualitatively or quantitatively, numerous aquatic insects depend entirely on hydrophyte tissues for food.

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THE OCCURRENCE OF *GYMNODINIUM BREVIS* IN THE WESTERN GULF OF MEXICO

Gymnodinium brevis Davis has been associated with mass fish kills in the Gulf of Mexico near the west coast of southern Florida since 1947, but has never been reported from other locations. Between 1948 and 1950 the U. S. Fish and Wildlife Service maintained a laboratory at Sarasota, Florida, and although numerous samples were collected throughout large areas of the adjacent Gulf waters during this period, *G. brevis* was not observed. In November 1952, a bloom of *G. brevis* which occurred in an area south and southwest of Sanibel Island was investigated by U. S. Fish and Wildlife Service personnel aboard M/V *Alaska*. From September 1953 to January 1955, *G. brevis* was found consistently in one location or another along the Florida west coast and since January 1955, it has been found sporadically and in low concentrations in that area.

During the period 1953-55, sea water samples were collected at Galveston, Texas and along the Gulf coast between Galveston and Florida, but no *G. brevis* were observed.

In September 1955, we investigated a fish kill near Port Isabel, Texas. Twelve samples were collected from an area of the Gulf of approximately 20 square miles between the mouth of the Rio Grande and a point approximately 10 miles north of Port Isabel. All of the samples contained *G. brevis* with concentrations ranging from 50 to 500 per milliliter. A sample collected near Port Isabel in Laguna Madre did not contain *G. brevis*. Fish were not dying at the time of our investigation, but dead fish extended along the Gulf beaches from the mouth of the Rio Grande to a point 17 miles north of Port Isabel.

C. E. Dawson and Henry Hildebrand at the Institute of Marine Science checked to a point 45 miles south of the Rio Grande along the Gulf Beach of Tamaulipas by air on September 15, 1955. Fish were observed dying and floating ashore in great numbers about 40 miles south of the Rio Grande. On the following day they checked 26 miles of beach from Playa Washington south and found dead fish in large quantities along 21 miles of beach. A water sample collected as a point 36 miles south of the Rio Grande contained a minimum of 22,000 *G. brevis* per milliliter. Information from fishermen and airplane pilots indicates at least 120 miles of coastline were affected in the state of Tamaulipas. Fish were still dying on September 27, 1955 along the Tamaulipas coast.

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DORMANCY IN THE SEED OF *CUSCUTA EUROPEA*

The species of dodder, *Cuscuta,* are numerous and circumboreal in their distribution. They are parasitic flowering plants, and many are extremely noxious weeds in crop plants such as flax, alfalfa, and clover. Recently, they have found use in experimental botany, where they provide a living bridge between non-related plants (Bennett 1940).

The seed of *Cuscuta* varies from species to species both in size and its ability to germinate. Although it is a mechanical obstruction that delays germination in one group of dodder species (Kinzel 1903, Gaertner 1950), there is at least one species, *C. europea* L., in which even a complete removal of the seed coat does not facilitate germination, and which, until this report, has not been known to germinate appreciably under any laboratory conditions. While, in the first group, a treatment with concentrated sulphuric acid for various periods (depending on the species and its age) will raise the germination from 2-5% to 80-100% (Gaertner 1950), *C. europea* will not respond to this or any other mechanical or chemical treatment. It was not until freshly harvested seed from the Gottenburgh Botanical Garden, Sweden, was flown to Canada in November, 1951, and stored immediately under various conditions in a refrigerator with temperatures ranging from —8° to +5° C., that considerable germination of this dodder was obtained.

The seed was stored in bulk under various storage conditions; samples were to be removed for germination tests at definite intervals. It was an unforeseen complication, when the seed started to germinate *in situ* at temperatures well below the optimum of 23-27° C. This unexpected germination could not be calculated on a common percentage basis because of the diminishing sample, and also the selection of the seed taken from the bulk for individual tests was affected by the accumulation of normally appearing seeds which proved to be without an embryo. Such seeds made up 64% of the sample tested after 8 months in storage. Johri and Tiagi (1952) in their morphological study of *C. reflexa* report exembryonate seed because the oospore nucleus failed to divide or curtailed its development shortly after its division. A similar condition with *C. europea* in this respect might be suggested.

None of the seed stored dry either in the laboratory or under refrigeration germinated when placed in a moist Petri plate at 27° C. during the 8-month period of study. Of approximately 2,800 seeds stored in moist peat at 0° C., 1,315 germinated *in situ,* and 558 during regular monthly germination tests. The remainder did not germinate because of insufficient stratification at the time of testing, or because the seeds were not viable. Of some 700 seeds stored over water at 0° C., 210 germinated *in situ,* and 410 during germination tests. After the 8-month study period, all the moist and cold stored seed material was exhausted.

Thus, *Cuscuta europea* will germinate readily at 27° C. after being stored immediately after harvest for at least 3 months in moist peat at 0° C. When the storage period is extended beyond this time, spontaneous germination will occur. In the samples studied, the number of seedlings obtained after a certain storage period could be ascertained by adding those that had germinated *in situ* to the figure obtained when placing seed under conditions best suited for germination. The optimum storage was thus determined as 5 months, moist and cold conditions. The stratified seed can be dried and stored in the laboratory without curtailing its germination ability, provided the embryo has not yet broken the seed coat, and is not thus directly exposed to desiccation.

The cold, moist storage would be variously effective depending on the age of the seed tested, and the period for which it was exposed to the moisture at low temperature. From the same lot of seeds, some germinated over 80%, when placed in moist cold storage as soon after harvest as possible, while others germinated only 36% after similar storage conditions, but following a delay of two years. Another sample of *C. europea* received from the Seed Laboratory in Wageningen, Holland, in August, 1953, and stored first for 2 months dry in the laboratory before the 5 months of cold, moist storage, gave only 50% germination.

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GRAZING EFFECTS ON COMPOSITION OF VIRGIN PRAIRIE IN NORTH-CENTRAL MISSOURI

Introduction

The extent of the prairie grasslands of the Midwest was noted often in the chronicles of early American explorations. Following a relatively short period of land use, compared to the time required for vegetational equilibrium, the pre-settlement prairie has been reduced to isolated tracts of small proportion. However, even these surviving examples of the original vegetation gradually are being destroyed by further encroachment.

The site of the present study is a 160 acre tract of unplowed tall grass prairie located in Callaway County in north-central Missouri. This particular area was described previously in a paper (Drew 1947), which presented the results of quadrat studies conducted during the period 1939-1942. Species composition of this prairie, moderately grazed and mowed for many years, was compared with ungrazed prairie fragments situated along railroad rights-of-way in the vicinity. Findings of this earlier study indicated that domestication caused a general increase in frequency and density of certain weedy species

and pasture grasses, and a decrease in various native species.

Since the termination of the 1939-1942 analysis, further changes in composition have been effected by fencing and the resulting differential treatment in grazing. Previously, the tract had been managed as a homogeneous entity. Beginning in the spring of 1941, one-half of the tract was not grazed but was utilized for hay. In this first year, these 80 acres of protected prairie produced 4,000 bales of forage. The remaining 80 acres were grazed through the summer from June to September, and mowed for the control of coarse plants. This practice of grazing one part of the prairie and not the other continued for 11 years. Approximately 50 cattle were carried seasonally. In recent years, utilization has increased with upward of 100 head being observed during the study.

At the present time, striking differences in physiognomy and composition exist between the two divisions, in which the grazed portion bears little semblance of prairie. It is the purpose of this paper to present quantitative comparisons in vegetation between the grazed and ungrazed portions.

Procedures

Field observations extended over a 4 year period with quadrat studies being conducted during a 3 week period in late May and early June of 1953. The two sections, grazed and ungrazed, were sampled separately for the determination of species frequency and cover dominance. Frequency of each species was calculated as the percentage ratio of quadrats in which species occurred to the total number employed. Species dominance was estimated as a percentage of total foliage cover in each quadrat, and expressed as an average of all samples. Later in the season, as flowering material became available, additional collections were made for positive identification of various specimens observed in quadrats. Although part of the study was conducted concurrently with grazing, no appreciable reduction in forage had yet occurred to alter the foliage cover estimates. A total of 48, 1 x 1 meter quadrats was employed in each of the two divisions. The species-area curve relationship indicated that this number, using meter square samples, exceeded the 5 per cent minimal area requirement.

Investigational Findings

The prairie portion protected from grazing during the 11 years, being more nearly similar to the homogeneous condition of the entire tract existing before fencing, provided a basis of evaluating composition changes in the seasonally-grazed section. Several changes attributable to grazing were noted. The most striking was the sharp reduction in vegetal cover of the native prairie grasses. In the protected area, prairie grass species comprised an estimated 68.5 per cent of the total vegetal cover. The percentage cover for these same species in the other portion, having approximately 11 years of grazing use, was reduced to 5 per cent. *Andropogon scoparius* which constituted 46.0 per cent of total herbaceous cover, or approximately 7/10 of the prairie grass cover, in the protected portion was reduced to an estimated 3 per cent by grazing. Similarly, frequency for this, the most common species was decreased from 98 to 27 per cent.

Various species other than grasses also were reduced in frequency and relative abundance, or were eradicated. Species absent under grazing included *Spiranthes cernua, Gentiana puberula, Lobelia leptostachys, Cacalia tuberosa, Senecio pauperculus,* and *Solidago gymnospermoides.* Included among the depleted species were *Amorpha canescens, Baptisia leucantha, Lespedeza capitata, Euphorbia corollata, Eryngium yuccifolium, Asclepias hirtella, Ruellia carolinensis,* and *Solidago nemoralis.*

This deterioration of the prairie was accompanied by a reciprocal increase in various species, including *Bromus commutatus, Hordeum pusillum, Cerastium vulgatum, Myosotis virginica, Plantago virginica, Houstonia mi-*

Table I. Comparison of frequency and cover of critically effected species in grazed and ungrazed portions of originally homogeneous prairie, 1953

Species	Frequency (%)		Estimated foliage cover (% of total vegetation)	
	Ungrazed	Grazed	Ungrazed	Grazed
Andropogon scoparius	98	27	46.0	3.5
A. gerardi	56	15	12.0	0.5
Sorghastrum nutans	50	15	4.4	0.5
Sporobolus heterolepis	44	0	4.5	0.0
Bromus commutatus	0	79	0.0	17.5
Hordeum pusillum	6	50	0.5	3.5
Cerastium vulgatum	10	83	0.5	3.0
Myosotis virginica	42	96	0.5	2.0
Plantago virginica	45	92	1.0	9.0
Houstonia minima	trace*	87	0.0	2.0
Antennaria neglecta	72	99	4.0	13.5

*Present in the area but not observed in quadrats.

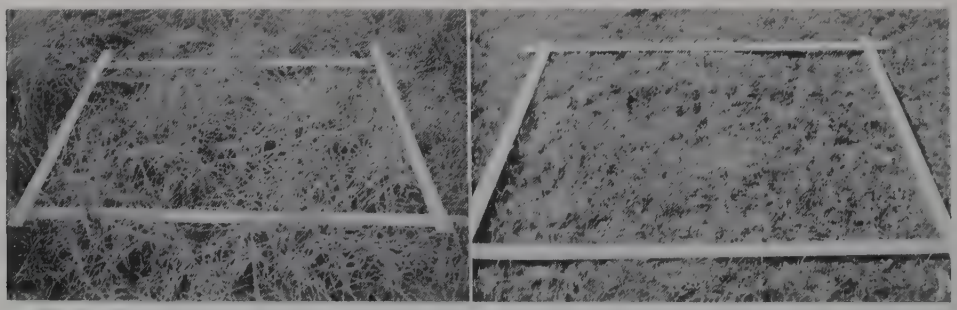

Fig. 1. Representative m² samples of vegetation in an originally homogeneous prairie. Left, ungrazed, with little bluestem the dominant species. Right, grazed for 11 years in which almost complete transformation in composition has been effected. Vegetation shown is in winter condition.

nima, and *Antennaria neglecta.* These species also were present in the tract protected from livestock but were not nearly so common. The drastic reduction of various species and the increase in others indicated livestock concentration as the primary causal factor. A summary of data pertaining to species undergoing greatest changes in frequency and cover values is presented in Table I. In Figure 1, representative portions of the study areas are shown in winter condition.

Due to varying phenologies of species growth, it is noted that cover estimates would vary with the period of sampling. However, it was thought that the May-June condition would give the best approximation of the potential cover. This was particularly necessary in the grazed section in order to make the study before utilization altered the foliage estimates. The species of replacement found under grazing generally resumed growth and produced green forage at an earlier date than did ungrazed prairie vegetation. The phenology of flowering in the grasses also differed, being vernal for the transformation species, including *Bromus, Poa,* and *Hordeum,* and midsummer for the prairie species typified by the *Andropogon* spp. In the fall, the prairie grasses became dormant early, with green forage persisting after frost only in the grazed section.

A 41 per cent reduction in number of species was observed in the deteriorated tract. Here only 67 herbaceous species appeared in quadrats in comparison with 115 species found in the intact prairie. While the latter presented a typical frequency distribution, the apparent effects of grazing reduced the percentage of species in the lower frequency classes, tending to equalize the class distribution. Thus, a simplification of the vegetation appeared as a result of disturbance associated with the grazing factor.

Several modifications were also noted in the intact portion of the prairie when present-day data were compared with those Drew gathered 15 years earlier One is the apparent spreading of *Danthonia spicata.* The change from 10 per cent frequency in 1939-1942 to the present 67 per cent represented a significant increase. The greater dispersion of this species was thought indicative of incipient deterioration and may be the result of a combination of disturbance factors including mowing and drought. Locally, the species occurs commonly on thin soils in open woods and glade prairies. Another difference found was the apparent decline of *Andropogon gerardi,* from an earlier frequency of 86 per cent (1939-1942) to the present 56. Photographs taken by Drew[1] at the time of his study indicated an earlier, more common distribution and a greater abundance. The high frequency (98%) of *Andropogon scoparius,* however, was maintained, although other prairie grasses showed some decrease.

Summary

This paper is a report of severe deterioration in native tall grass prairie in Central Missouri. Grazing and trampling by livestock were indicated as paramount factors in the decline, although mowing and prolonged drought were sustaining causes. Sharp reductions in *Andropogon* spp., and other prairie grasses were observed and measured quantitatively. The widespread increase of several invaders, including *Bromus commutatus, Hordeum pusillum,* and *Antennaria neglecta* occurred as disturbance continued.

Another effect associated with the grazing factor was reduction in total number of species, under the observed conditions a decrease of 41 per cent. Intensive utilization by domestic livestock was shown as an effective factor in modifying the original prairie composition in a relatively short period of time.

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[1] Obtained through personal correspondence, the use of which is gratefully acknowledged.

DISTRIBUTION OF DISTANCE TO NTH NEIGHBOUR IN A POPULATION OF RANDOMLY DISTRIBUTED INDIVIDUALS

Introduction

Clark and Evans (1954) have devised a procedure for using the distance to nearest neighbour as a measure of the departures from randomness in a population of plants. Although mentioning the extension to second, third, etc. nearest neighbours as a possibility, they considered that the formulae for these cases would be more complex than those used in their paper, and did not attempt any further investigation. The extension is, in fact, quite simple, and the resulting formulae are of the same form as the nearest neighbour case. The mathematical derivations are given in an appendix, and it is shown there that the distributions of distances to neighbours of all orders are related to the χ^2 distribution.

In a little-known paper[1] published in Japan, Morisita (1954) has derived the same formulae, in a somewhat different manner, however, and without demonstrating the general nature of the distributions. He uses the information, combined with other methods (such as distance to nearest neighbour in each of four quadrants) to obtain densities of random populations, but the applicability of the results to non-random distributions is very doubtful. In the present work, the emphasis is on the use of the method for describing aggregation in plant communities and so detecting non-randomness. The advantage in using second, third, etc. nearest neighbours (apart from the in-

[1] The author wishes to thank the referee for drawing his attention to this reference.

crease in accuracy of density determination in a random population, pointed out by Morisita) is that it should be possible to detect larger-scale heterogeneity than by merely using the distance to the nearest neighbour.

Tests of Significance

Let the population of individuals be distributed randomly with density m per unit area. Let $\lambda = \pi m$, so that λ is the mean number of individuals in a circle of unit radius. Then the distribution of the distance r_n to the nth nearest neighbour is (see appendix)

$$P(r_n) = 2\lambda^n e^{-\lambda r_n^2} r_n^{2n-1} dr_n/(n-1)!,$$

and if we put $2\lambda r_n^2 = x_n$, the distribution of x_n is

$$P(x_n) = e^{-\frac{1}{2}x_n}\left(\frac{x_n}{2}\right)^{n-1} dx_n/(n-1)!,$$

which is a χ^2 distribution with 2n degrees of freedom. It follows that in a sample of size N, the statistic $N\bar{x}_n$, where $\bar{x}_n$ is the mean of the N observed values of $\bar{x}_n$, is distributed as χ^2 with 2Nn degrees of freedom, and so we have immediately a simple test of the randomness or otherwise of a given distribution of distances. A probability of χ^2 greater than 0.95 indicates significant overdispersion of individuals, the distances being smaller than expected, while a probability less than 0.05 indicates significant underdispersion. We can also, if desired, derive limits for the expected mean $E(\bar{x}_n)$, if the population is random, using the normal approximation to the χ^2 distribution (valid if the degrees of freedom are fairly large). The 95% limits for $E(\bar{x}_n)$ are given by

$$(\sqrt{(4Nn-1)} \pm 1.96)^2/2N,$$

where 1.96 is the deviate corresponding to a probability of 0.05 in the two tails of the normal distribution. In practice, then, we would estimate $\lambda_o = \pi m_o$, where m_o is the observed density of plants, calculate the mean $\bar{x}_n$ of N observed quantities $2\lambda_o \bar{r}_n^2$ and compare it with the expected limits under the hypothesis of randomness.

A more approximate procedure can be devised using the untransformed distances r_n; this is the method given by Clark and Evans for the distance to nearest neighbour r_1. It consists in regarding the distribution of r_n as approximately normal, and applying ordinary normal probability theory to the mean $E(r_n)$ and standard deviation $\sigma(r_n)$. The moments and moment-constants of the distribution of r_n for $n = 1, 2, 3, 4$ are given in Table I, and these show the distribution to be rather skew for low values of n, but to tend to normality as n increases. For n very large, $E(r_n) \to 0.5642\sqrt{(n/m)}$, (see appendix), $\sigma(r_n) \to 0.5/\sqrt{\lambda} = 0.2821/\sqrt{m}$, (this may effectively be taken as the value of $\sigma(r_n)$ for $n > 4$), $\beta_1 \to 0$, $\beta_2 \to 3$. Approximate 95% limits for the expected mean of a sample of N observations from a random population would be given by

$$E(r_n) \pm 1.96\,\sigma(r_n)/\sqrt{N}.$$

Alternatively, the statistic

$$c = \frac{\bar{r}_n - E(r_n)}{\sigma(r_n)/\sqrt{N}},$$

where $\bar{r}_n$ is the mean of N observed values of r_n, can be taken approximately as a normal deviate and tested against the probability levels of the normal distribution. More reliance should, however, be placed on tests employing the χ^2 distribution.

Table I. Moments and moment-constants of the distribution of r_n

n	1	2	3	4
$E(r_n)$	$\frac{0.5000}{\sqrt{m}}$	$\frac{0.7500}{\sqrt{m}}$	$\frac{0.9375}{\sqrt{m}}$	$\frac{1.0937}{\sqrt{m}}$
$\sigma(r_n)$	$\frac{0.2614}{\sqrt{m}}$	$\frac{0.2723}{\sqrt{m}}$	$\frac{0.2757}{\sqrt{m}}$	$\frac{0.2774}{\sqrt{m}}$
β_1	0.644	0.406	0.318	0.269
β_2	3.245	3.059	3.025	3.105

Examples and Discussion

To illustrate the procedures involved in applying the above tests of significance, two examples are given. The first is a synthetic random distribution constructed by taking groups of random digits for the co-ordinates of the positions of the plants. 100 points were placed on a grid of 400 quadrats each half an inch square and 25 were selected at random as centres of measurement. The second was taken from the mapped distribution of individuals of *Solidago rigida* given in Cain and Evans (1952), an area of 50 quadrats each 5 metres square containing 105 plants being chosen and a sample of 25 centres selected at random. In each case, the side of the quadrat was taken as the unit of measurement. The results are presented in Table II.

Although these samples are perhaps too small to draw valid conclusions from, it would appear that in the *Solidago* distribution non-randomness is demonstrated by the distances to the nearest neighbour and possibly the second-nearest, these being smaller than expected on the hypothesis of randomness. A larger sample might possibly have detected departures in the more distant neighbours. The results generally follow expectation on the basis of previous studies, Cain and Evans describing the distribution as consisting mainly of

TABLE 2. Tests of significance on two distributions

n	1	2	3	4
A. Synthetic random: $m_0=0.25$, N=25				
$N\bar{x}_n=\chi^2$	55.63	99.85	130.47	192.99
d.f.	50	100	150	200
Probability	0.25	0.50	0.87	0.59
$\bar{x}_n$	2.23	3.99	5.22	7.72
95% limits for $E(x_n)$	1.28	2.95	4.70	6.49
	2.84	5.16	7.41	9.62
$E(r_n)$	1.0000	1.5000	1.8750	2.1875
$\sigma(r_n)$	0.5228	0.5446	0.5514	0.5548
95% limits for $E(r_n)$	0.7950	1.2866	1.6588	1.9699
	1.2050	1.7134	2.0912	2.4051
$\bar{r}_n$	1.0900	1.5468	1.7696	2.1756
c	0.44	0.23	0.49	0.03
Probability	0.66	0.82	0.62	0.98
B. *Solidago rigida*: $m_0=2.10$, N=25				
$N.\bar{x}=\chi^2$	33.02	80.38	157.86	201.56
d.f.	50	100	150	200
Probability	0.97	0.92	0.32	0.46
$\bar{x}_n$	1.32	3.21	6.31	8.06
95% limits for $E(x_n)$	1.28	2.95	4.70	6.49
	2.84	5.16	7.41	9.62
$E(r_n)$	0.3450	0.5175	0.6469	0.7548
$\sigma(r_n)$	0.1804	0.1879	0.1903	0.1914
95% limits for $E(r_n)$	0.2742	0.4438	0.5722	0.6797
	0.4158	0.5912	0.7216	0.8299
$\bar{r}_n$	0.2632	0.4648	0.6336	0.7228
c	2.27	1.40	0.35	0.84
Probability	0.02	0.16	0.67	0.40

minor clumps and scattered individuals and pairs. In a purely hypothetical example in which individuals are aggregated in randomly scattered clumps, then depending on the average number of individuals per clump, we might expect to find departures from randomness in the first few distances and an approach to randomness thereafter. The problem of determining the exact distribution of distances to neighbours in non-random models is one which still requires attention but which appears very difficult of solution. However, the method described above is valuable in that it indicates to a greater degree than is possible using only the nearest neighbour, the nature as well as the degree of non-randomness present in a plant community.

APPENDIX

Distribution of r_n

In a population of individuals distributed randomly with density m per unit area, the probability of x individuals falling in any area of unit size is obtained from the Poisson series, and is $m^x e^{-m}/x!$ The number of individuals in a circle of radius r will follow a Poisson distribution with mean $\pi r^2 m$, which we write λr^2. Now if a random individual is taken as centre, the probability that no individual occurs inside a circle of radius r_1, written $P(O \text{ in } (O, r_1))$, is

$$P(O \text{ in } (O, r_1)) = e^{-\lambda r_1^2}.$$

(the first term of the Poisson series). The probability that at least one individual occurs in the annulus between the concentric circles radii r_1 and R_1, written $P(> O \text{ in } (r_1, R_1))$, is

$$P(> O \text{ in } (r_1, R_1)) = 1 - e^{-\lambda(R_1^2 - r_1^2)}$$
$$\rightarrow 2\lambda r_1 \, dr_1 \text{ as } R_1 \rightarrow r_1.$$

Therefore, the probability that the nearest neighbour is distant r_1 from the centre, written $P(r_1)$, is

$$P(r_1) = e^{-\lambda r_1^2} 2\lambda r_1 \, dr_1,$$

as obtained by Clark and Evans.

Continuing in a similar manner and writing $P(r_2 \mid r_1)$ for the probability that the second nearest neighbour is distant r_2 given that the nearest neighbour is distant r_1, and $P(r_1, r_2)$ for the joint probability that the nearest neighbour is distant r_1 and the second nearest distant r_2, we have

$$P(O \text{ in } (r_1, r_2)) = e^{-\lambda(r_2^2 - r_1^2)}$$
$$P(> O \text{ in } (r_2, R_2)) = 1 - e^{-\lambda(R_2^2 - r_2^2)}$$
$$\rightarrow 2\lambda r_2 dr_2 \text{ as } R_2 \rightarrow r_2,$$
$$P(r_2 \mid r_1) = e^{-\lambda(r_2^2 - r_1^2)} 2\lambda r_2 dr_2,$$
$$P(r_1, r_2) = P(r_1) \cdot P(r_2 \mid r_1)$$
$$= e^{-\lambda r_2^2} (2\lambda)^2 r_1 r_2 dr_1 dr_2.$$

For the third nearest neighbour

$$P(O \text{ in } (r_2, r_3)) = e^{-\lambda(r_3^2 - r_2^2)}$$
$$P(> O \text{ in } (r_3, R_3)) = 1 - e^{-\lambda(R_3^2 - r_3^2)}$$
$$\rightarrow 2\lambda r_3 dr_3 \text{ as } R_3 \rightarrow r_3,$$
$$P(r_3 \mid r_1, r_2) = e^{-\lambda(r_3^2 - r_2^2)} 2\lambda r_3 dr_3,$$
$$P(r_1, r_2, r_3) = e^{-\lambda r_3^2} (2\lambda)^3 r_1 r_2 r_3 dr_1 dr_2 dr_3.$$

From these results it is quite easy to obtain the general result

$$P(r_1, r_2, \ldots, r_n) = e^{-\lambda r_n^2} (2\lambda)^n r_1 dr_1 r_2 dr_2 \ldots r_n dr_n,$$

where $O \leqq r_1 \leqq r_2 \leqq \ldots \leqq r_n$. The absolute probability that the nth nearest neighbour is distant r_n from the centre, written $P(r_n)$, is obtained by integrating the general result successively with respect to r_1 from O to r_2, w.r.t. r_2 from O to r_3, . . . , w.r.t. r_{n-1} from O to r_n, and is

$$P(r_n) = 2\lambda^n e^{-\lambda r_n^2} r_n^{2n-1}\, dr_n/(n-1)!,$$

showing that $2\lambda r_n^2$ is distributed as χ^2 with 2n degrees of freedom.

The mean distance to the nth nearest neighbour is

$$E(r_n) = \int_0^\infty r_n P(r_n)$$
$$= \sqrt{\frac{\pi}{\lambda}} \cdot \frac{(2n)!\,n}{(2^n \cdot n!)^2}$$
$$= \frac{1}{\sqrt{m}} \frac{(2n)!\,n}{(2^n \cdot n!)^2}$$

The second moment is

$$E(r_n^2) = \int_0^\infty r_n^2 P(r_n)$$
$$= \frac{n}{\lambda}$$

We can find the ratio of $E(r_n)$ to $E(r_1)$ as n increases, using Stirling's approximation. We have

$$E(r_n)/E(r_1) = (2_n)!\,2n/(2^n \cdot n!)^2$$
$$\to 2\sqrt{(n/\pi)}, \quad \text{which is approximately equal to} \quad 1.13\sqrt{n},$$

so that the area of the circle containing the nth nearest neighbour on its circumference is expected to be approximately n times as large as the area of the circle with the nearest neighbour on its circumference. In other words, the series of radii $E(r_n)$ describe concentric circles with annuli of approximately equal area, as might be expected intuitively.

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INFLUENCE OF MAN ON VEGETATION AND ENVIRONMENT 2,300 YEARS AGO[1]

"There are mountains in Attica which can now keep nothing but bees, but which were clothed, not so very long ago, with fine trees producing timber suitable for roofing the largest buildings, and roofs hewn from this timber are still in existence. There were also many lofty cultivated trees.

The annual supply of rainfall was not lost, as it is at present, through being allowed to flow over a denuded surface to the sea, but was received by the country, in all its abundance—stored in impervious potter's earth—and so was able to discharge the drainage of the heights into the hollows in the form of springs and rivers with an abundant volume and wide territorial distribution. The shrines that survive to the present day on the sites of extinct water supplies are evidence for the correctness of my present hypothesis."

Plato (427-347 B.C.)
Critias

[1] Anonymous. 1955. Sierra Club Bull. **40** (4): 31.

REVIEWS

In Honorem Septuagenarii J. Braun-Blanquet[1]

A volume of more than 600 pages has been issued as a testimonial to J. Braun-Blanquet on the occasion of his seventieth birthday. This constitutes the 5th and 6th volumes of *Vegetatio,* a periodical founded in 1948 by Braun-Blanquet himself with the aid of some of his most faithful followers, especially the Dutch de Leeuw, Heimans, Barkman and others, in whose care the editorial work has been placed. The current secretary is H. W. Mullenders of Louvain, Belgium. The list of editorial collaborators is truly international and includes quite a few names of ecologists who hardly subscribe to the doctrine of the Zürich-Montpellier School, although most of them can be considered "sympathizers." In fact, in its four previously published volumes, *Vegetatio* has printed a majority of papers written by members of the School, but not a few others by writers who had adopted a somewhat different approach.

This is hardly the place to re-state the tenets of Braun-Blanquet's School of phytosociology; its positions are well known from Conard and Fuller's able translation of the first edition of "Pflanzensoziologie" and from Oosting's re-statements in his current textbook. The history and philosophy of the school, its failure to strike roots in the English-speaking world are another matter which the present volume almost inescapably brings up. Although one can hardly fail to perceive the dogmatic or at least the polemic note in some of Braun-Blanquet's writings, one cannot overlook the equally militant attitude of many who have opposed his views, often without having truly understood the self-imposed limitations of the School.

The basic assumptions or emphases of the system, if they can be summarized, concern the following points: 1) over-all indicator value of floristic assemblages, even without benefit of detailed recording of ecological factors or of vegetation structure; 2) cohesion of association-complexes; 3) organismic nature of the association; 4) regional importance and bioclimatic significance of the higher phytosociological units.

The field methods of the School are yet another matter, since they do not require strict adherence to a univocal scientific philosophy but lend themselves, in practice, to many applications.

Quite apart from their intrinsic value, therefore, the papers collected in this volume offer a panorama of the range of Braun-Blanquet's influence, since it can be said that the contributors implicitly recognize a greater or lesser debt to the master, whether they have followed somewhat closely in his footsteps, like Tüxen, Bolòs, Soó, Molinier, Nordhagen, and Etter, or have integrated some of his concepts and procedures into quite a different system, like Hosokawa, Lucy Moore, Suzuki-Tokio, Boyko, Bouillenne, Böcher, Iversen. Some of the contributions, however, are merely a tribute to Braun-Blanquet and show no obvious relation to his work and his ideas. Such are Sir Arthur Tansley's pleasant but noncommittal "reminiscence" and papers by Kalela, Phillips, Vaarama, Du Rietz, Heimans, Richards, and others.

[1] Vegetatio, Acta Geobotanica. 1954. Vol. V-VI. xii + 606 pp. Den Haag: Junk. Dutch guilders 60.— ($15.80).

In tracing Braun-Blanquet's influence in these many and diverse texts, one must not look only for the association-charts with their taxonomic hierarchy of associations fitted into alliances and these into orders, etc. A close reading of Braun-Blanquet recalls to memory his preoccupation with two other aspects of geobotany: historical plant geography and autecology (see the many contributions by his students in the *Communications de la Station Internationale de Géobotanique Méditerranéenne et Alpine,* a collection of about 120 papers unfortunately not to be found in many American university libraries). Contributions by des Abbayes, Löve, and Conard reflect the floristic leaning, whereas those by Watt, de Vries and Venema, Simons and Ellenberg are concerned with autecology.

Altogether there are 72 contributions by 81 authors from 25 countries. All parts of the world are represented, but Western Europe predominates: Germany has 13 papers, Switzerland 8, Holland 7, Belgium 6, Scandinavia 6, France 4, Austria 3, Spain 3. North America has only 2, and all the other countries have 2 or 1: Algeria, Czechoslovakia, England, Gold Coast, Hungary, India, Indonesia, Israel, Japan, New Zealand, Portugal, Turkey, Yugoslavia.

What this volume does demonstrate is that, whatever the limitations of the methods of the Montpellier School, they are not necessarily such as to invalidate application to a very broad range of vegetation types: wet tropical (Emberger, Lebrun, Léonard, Bharucha), dry tropical (Walter, Zohary and Orshan), wet temperate (Moore), as well as the Alpine, Mediterranean and medio-European. It is certainly most useful to have this volume now, as a compendium of current thinking on the part of the Zürich-Montpellier school. The many ideas which have been proffered and used by this group through the years are all represented here. Some of them are possibly now past their "optimal phase," and new ones are emerging. In the work of Tüxen, Westhoff, Emberger, Hosokawa (and also of Rivas Goday and of Mangenot, who unfortunately are not represented here), new trends are evident: there is less emphasis on the floristic aspect and less confidence in the over-all indicator value of small constellations of plant species, and more weight is given to environmental controls and to vegetation structure.

Those who, like myself, came early under the influence of Josias Braun-Blanquet and were initiated to his approach in the field, carry a great debt. We may have felt, even as young men, that "the School" was more demanding than a scientific system has a right to be. We could hardly help being impressed with the tremendous and detailed knowledge of plants that the master demonstrated in the field. His taxonomy was always painstaking and reached down to the level where the geneticists were beginning to urge us to stoop. In fact, a great deal was accomplished very close to the ground and through intimate contact with plants on those field trips through the Cévennes and the Alps. We also felt that a solid knowledge of historical plant geography and of physiological requirements supported Braun-Blanquet's estimations of the "characteristics" which he assembled into associations.

Certainly his enthusiasm made us want to see his system "from the inside" and make our own assay of it. Those of us who later have not held to the line of orthodoxy nevertheless have learned a great deal and can continue to apply in a different context a good many of the School's concepts. Above all, contact with Braun-Blanquet was a rewarding and exemplary experience as must be all contact with a perceptive and critical mind that is sustained by great warmth and kindliness.

The present book stands as a tribute of high quality, and was presented by the contributors during the VIIIth International Botanical Congress in Paris during the summer of 1954.

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In Honor of Erwin Aichinger[1]

The marked expansion of ecological research on the Continent since the war has been accompanied by the establishment of several new journals. One of these is *Angewandte Pflanzensoziologie* [Wien], a series published by Springer for the Institut für Angewandte Pflanzensoziologie des Landes Kärnten and edited by the Austrian student of the applied phytosociology of forests, Erwin Aichinger. In honor of Aichinger's 60th birthday, a special volume of this series has been issued, edited by E. Janchen with the assistance of A. Gayl and G. Wendelberger. Phytosociologists and ecologists from all over the world have contributed to a massive, two-volume *Festschrift* of 1310 pages and 95 papers. An American may well be amazed at the scale of such a work, especially in contrast with the limited memorial Americans recently dedicated to their greatest plant ecologist, F. E. Clements. Of the many papers included, it is clearly impossible to mention more than a few which were of special interest to the reviewer.

There are many papers on forest ecology and phytosociology. The largest share of these represent central Europe and the school of Braun-Blanquet; but there are also papers of interest on forests of the Harz Mountains by Meusel, on site-types of Scandinavian beech forests by Lindquist, and others. Two papers on forest typology are of special interest in presenting, in German, the current viewpoints of eminent authors behind the Iron Curtain. The dean of Russian forest phytocenology, W. N. Sukatschew, gives the perspective from a lifetime's study in "Die Grundlagen der Waldtypen." Sukatschew's conception of the forest (like that of his predecessors Morosov and Krüdener) is ecosystemic; the forest is interpreted as a "biogeocenose." The forest-type is consequently a biogeocenose-type, a grouping of forest stands which are similar in composition of trees and other layers, in animal communities and the whole complex of environmental conditions, and in processes of interaction, reproduction, and succession, and which consequently require uniform management. Sukatschew further views forests as in unceasing change and movement, in which the different types and rates of change are not generally separable in the field. In such landscapes in flux there is little question of an ultimate, climatic type.

A. Zlatník, in "Methodik der typologischen Erforschung der čechoslowakischen Wälder," observes that nationalization of industries and estates in Czechoslovakia has given the prerequisites for a large-scale, unified state forest-management plan. The plan and the approach to forest classification are described in some detail. All the plants of concern are compared according to 20 ecological characters to seek groups of species which are ecologically similar. Of most value for classification are not character-species, but differential-combinations, groups of differential-species of the same synusiae. By averaging the representation of various differential-combinations in similar stands, a "model" of the forest community-type can be obtained. The forest-type is a totality of natural and disturbed biocenoses and environments, presumably of the same origin and close similarity of site conditions, and characterized above all by type of undergrowth. These two papers, which may have a semi-official character for the Communist area, are alike in stressing the need for cooperative, team research into forests and their environments. Actual accomplishments of their inter-disciplinary, ecosystemic approach are yet to be seen.

E. Klapp, R. Knapp, D. M. de Vries, and a number of others have contributed papers on the ecology of grasslands. Most of these follow the school of Braun-Blanquet; but the paper of de Vries, who does not, is of special interest in bringing together work on grasslands which this outstanding Dutch student and his associates have published in many, scattered, short papers in three languages.

Two essays of significance on ecological theory are H. Walter on "Klimax und zonale Vegetation" and H. Ellenberg on "Zur Entwicklung der Vegetationssystematik in Mitteleuropa." Walter has previously expressed the monoclimax theory in its Russian form, and in this paper carries it to its logical conclusion. He argues that it is necessary to free the climax concept from its hypothetical involvements by separating it completely from the concept of succession. By *climax-community* we may then understand only those undisturbed communities which achieve predominance over an extensive area with uniform climatic relations. For suppositious ultimate stability, *regional* or *zonal prevalence* is substituted as the primary criterion of climaxes. It is further suggested that climax communities develop most typically on deep, loamy soils, and apparently accepted that mountains must be largely left out of consideration. In avoiding the monoclimax confusion of stability and prevalence, ecologists may prefer to associate the term *climax* primarily with stability and to seek a concept applicable to both mountains and plains. But Walter's is a third possibility in solution of the climax dilemma, along with the two others recently offered in this country.[2]

Ellenberg writes of some basic problems of community classification and the current "crisis of the character-species doctrine." He observes that as knowledge of the plant communities of central Europe increases, the num-

[1] Festschrift für Erwin Aichinger zum 60. Geburtstag. 1954. Sonderfolge der Schriftenreihe *Angewandte Pflanzensoziologie*. 2 vols., xxxii + 1310 pp. Wien: Springer-Verlag. DM 90.— ($21.40).

[2] Whittaker, R. H. 1953. Ecol. Monog. 23: 41-78. Dansereau, P. 1954. Ecology 35: 575-579.

ber of good character-species, and consequently the significance of the fidelity concept for vegetational systematics, is progressively reduced. The problems thus raised suggest fundamental change in classification at lower levels: abandonment of the definition of associations by character-species, or local characterization of the association within a broader unit such as the *Hauptassoziation* of Knapp, or, as Ellenberg prefers, a flexible characterization of lower units emphasizing distributional groupings or *ecological groups*. Ellenberg has done some striking work in gradient analysis,[3] and his viewpoint is suggestive of that of Americans associated with this approach. His paper suggests some fundamental reservations about the system of Braun-Blanquet, but without offering much comfort to ecologists who oppose this system; he points out also the limitations of approaches through dominance and physiognomy.

Two of the longest papers are vegetation studies by G. Wendelberger, "Steppen, Trockenrasen und Wälder des pannonischen Raumes," and P. Zangheri, "La vegetazione della Romagna (Italia centro-settentrionale)." Wendelberger's is a very interesting study from different viewpoints of a number of central European grassland communities, an example of productive use of the system of Braun-Blanquet in a study that goes far beyond formal classification for its own sake. Zangheri's approach is influenced less by Braun-Blanquet than by another school of Zürich-Montpellier, that of Schmid. While granting limitations of the monoclimax theory, Zangheri recognizes four *climax areas* in the Romagna, each characterized by the prevalence of a given dominant species—*Quercus robur, Q. ilex. Q. pubescens*, and *Fagus silvatica*. This approach toward regional vegetation types may be of interest to Americans as suggestive of their own "climax associations," since these and related units are accepted by no one on the Continent. Zangheri's and other impressive current Italian work may also have increased interest to Americans when vegetation of comparable climates in California is more actively studied.

D. W. Goodall has contributed a penetrating paper on the statistics of stand homogeneity and "Vegetational classification and vegetational continua"; R. H. Whittaker has written on genetic and theoretical aspects of the indicator problem, "Plant populations and the basis of plant indication." There are, however, only a few papers by English-language ecologists and fewer by Scandinavian phytosociologists. Although papers are contributed from, or deal with, countries as far from Europe as New Zealand, Japan, Argentina, India, and the Gold Coast, the bulk of the papers are from middle and southern Europe. The special value of the *Festschrift* for ecologists is in providing a representation of current basic and applied phytosociology in this area, where vegetation research is being carried on more intensively than anywhere else in the world, such as can scarcely be found together elsewhere. The *Festschrift* is further valuable for a number of papers of distinctive merit or significance contributed to it. Ecologists may well congratulate both Dr. Erwin Aichinger on his 60th birthday, and the editors for the impressive form in which they have honored it.

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[3] Ellenberg, H. 1950. Landwirtschaftliche Pflanzensoziologie. I. Unkrautgemeinschaften als Zeiger für Klima und Boden. 141 pp.
———. 1952. Landwirtschaftliche Pflanzensoziologie. II. Wiesen und Weiden und ihre standörtliche Bewertung. 143 pp. Stuttgart/z.Z. Ludwigsburg: Eugen Ulmer.

Imbalance between Man and Environment[1]

Thinking scientists, at least, cannot view the facts of population pressure in relation to natural resources without accepting in principle the ideas of Tertullian (third century A.D.) and Malthus (1798). In 1948, William Vogt in *Road to Survival* (William Sloane Associates) and Fairfield Osborn in *Our Plundered Planet* (Little, Brown and Co.) shocked the lay public to serious thought about interrelationships between man and his environment. Since then several excellent books supporting the principles propounded have appeared, including *Human Fertility: The Modern Dilemma* by Robert C. Cook (1952, William Sloane Associates) and *The Next Million Years* by Charles D. Darwin (1952, Rupert Hart-Davis). The beneficial impact of these books has been counteracted by such books as *Enough and To Spare* by Kirtley F. Mather (1944, Harper and Brothers) and *The Road to Abundance* by Jacob Rosin and Max Eastman (1953, McGraw-Hill) in which complacent confidence is placed in man's superior intelligence to solve his population and resource problems. The three complementary books reviewed here provide concepts as close to realism as one is likely to get. What one book fails to do, one of the others accomplishes.

Fairfield Osborn, currently president of both the New York Zoological Society and the Conservation Foundation, has a stimulating, thought-provoking style. His penetrating analyses force upon the reader a clear understanding of relationships between human populations now and during the historic past. The analyses of Greek, Roman, Spanish and British cultures are especially good in demonstrating precisely that populations of man have been controlled repeatedly by Malthusian "positive" checks. Particularly significant are the chapters on Africa and the Amazon, the two sizable land areas to which optimistic demographers would like to turn to settle the problem of excessive human populations. Infertile, lateritic soils; severe erosion on arable land; overgrazing by livestock; and destruction of native wild animals, coupled with racial problems, limit the productivity of the huge African continent to little more than its present level. Osborn's vivid description of the Amazon makes it easy to understand why this immense region has remained almost as unproductive as it was four centuries ago. Most of the Amazon basin is suitable only for tree crops; cultivation is confined to streambanks. The 1,000 million acres of tropical land which Robert M. Salter and others visualize as potentially cultivatable do not exist. Sax is is agreement with Osborn; Brown is inclined to accept

[1] Osborn, Fairfield. 1953. The limits of the earth. x + 238 pp. Boston: Little, Brown and Co.
Brown, Harrison. 1954. The challenge of man's future. xii + 290 pp. New York: Viking Press.
Sax, Karl. 1955. Standing room only. 206 pp. Boston: Beacon Press.

Salter's figures. The delusion of food surpluses in the United States, Canada, New Zealand, Australia, and Argentina is emphatically presented by Osborn, especially with reference to the ever-widening gap between increase in food production and increase in population. From the average for the years 1934-1938 to the levels attained in 1953, world population increased 12 per cent while food production increased only 9 per cent. The President's Materials Policy Commission of 1952 is referred to extensively by all three authors for evidence showing that the United States is outgrowing its resource base. By 1975 the demand for minerals will increase by 90 per cent, timber products by 10 per cent, and agricultural products by 40 per cent. The demand for energy will double and the need for water for industrial needs alone will treble. Since World War I the United States has used more metals and mineral fuels than the total used throughout the entire world in all history preceding 1914.

Sax, professor of botany at Harvard University, is gratifyingly clear on the entire subject matter and in particular on Malthusian principles, demographic areas of the world, the importance of achieving world-wide Demographic Transition, and food potentialities. Conclusions are formulated on the basis of careful analyses of relevant facts, most of which are well presented in tabular or graphic form. More attention is given to the dynamics of human populations than in perhaps any other popular account. Emphasis is placed on (1) the fact that high birth rate was essential to compensate for high death rate in primitive human populations, and (2) that our present dilemma arises from reducing death rate by about one-third without corresponding reductions in birth rate. Comparison of land needed for specific diets is based on "original calories" which include energy utilized by livestock. People in the United States are still wasteful, using 10,000 original calories per person when the same level of nutrition could be maintained on 5,000 to 6,000 original calories. Being a botanist, Sax is in a position to evaluate the potentialities of food production better than most scientists. For many decades the living plant must provide "our daily bread." Limitations of yeast and Chlorella culture in providing additional food for the world are more realistically presented by Sax and Osborn than by Brown. Present availability and future potentialities of energy needed for an industrial culture are carefully discussed by Sax and Brown. At current rates of population increase and energy consumption, demands for energy would be increased twentyfold by the year 2050. Coal reserves cannot meet the demands for energy in the near future. Both authors agree that full development of water-power resources would provide only a small fraction of the world's need. The discussion of energy is one of the best parts of Brown's book. One might anticipate this from the fact that Brown is a physical chemist at California Institute of Technology and was formerly a member of the staff of the Institute for Nuclear Studies of the University of Chicago.

When the rich ores of uranium and thorium are exhausted, ordinary granite can be processed to yield a per ton *net* equivalent of the energy in about seven tons of coal. To provide from granite the uranium and thorium "capital" in atomic reactors required by a world population of seven billion persons, who consume energy at a per-capita rate equivalent to that derived from burning 10 tons of coal annually, *1000 cubic miles* of rock would be needed and 6.4 billion tons of rock would have to be processed annually. Disposal of radioactive wastes would be a major, if not limiting, problem in the use of atomic energy. Sax points out that if energy could be made available through nuclear fusion, as in the hydrogen bomb, our energy requirements would be solved indefinitely. Limitations of iron ore and indispensable metals, such as copper, tungsten, nickel, cobalt, chromium, lead, and tin are recognized by all three authors as a formidable barrier to world development. To keep up the supply requires ever-increasing expenditures of energy. From the point of view of energy, Brown believes a population level of seven billion persons could, in principle, be supported. From a nutritional point of view, assuming people are willing to eat foods that bear little resemblance to foods now eaten, Brown can visualize a population of 50 billion persons, a view not shared by Sax and Osborn. But the world in which Brown would like to live supports much lower population levels and blends man's creativity with the creativity of nature. "Man, in this world, lives in balance with his environment, nourished by nature in harmony with the myriads of other life forms that are beneficial to him."

An excellent philosophical discussion of man's probable future is presented in Brown's final chapter. The most likely pattern is a reversion to an agrarian culture as a result of war or exhaustion of iron ore or other metals before conversion to use of low-grade ores with sufficient supplies of energy are achieved. The probability of a second emergence of industrialized civilization following war is remote. Sax and Brown agree that the greatest obstacle in achieving a favorable ratio of human populations to natural resources lies in the enormous population pressures, arising from the inevitable, rapid population growth, during the period in which 85 per cent of the world population attempts Demographic Transition. Obviously, birth control must be established to limit population increase. Best discussions of this topic are by Sax, with the proposal that a steroid compound which prevents ovulation be added to a staple food and consumed by everyone except women planning to have children. Although the possibility still exists today that populations of man can be brought into proper relationship to his environment, the fulfillment of this possibility is remote if current trends in population increase and food and energy consumption continue into the near future.

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A Theory of Human Population Limit[1]

The American dream (and obsession) to create an ever-higher level of living for all mankind is being realized—but at the price of resource capital. The price may be more than the United States can afford. ". . . continuing and increasing consumption of raw materials due to economic expansion is proportionally far greater than the population rise." The limit of population growth will be determined, according to Ordway's theory, when basic resources come into such short supply that rising costs will make their use in additional production unprofitable and industrial expansion stops. The significant role of increased needs in terms of energy to extract resources in short supply was not developed. Raw materials needed for industry, rather than food, will limit population size. However, the food barrier is not neglected. Since 1945, our food production has increased 50 per cent less than our population. Acres of arable land per person have decreased from 3.26 in 1920 to 2.25 in 1950. By 1975 there will be a need for 116 million acres of additional cropland, or its equivalent, in terms of increased production on existing lands. Technologists believe not more than an equivalent of 70 million acres of nonexisting new acres can be made up through application of all known agricultural improvements. Only 17.2 million acres are available all together for irrigation; about 1/3 of these have been developed. The philosophy of inexhaustible raw materials and limitless population growth needs severe censure if the American dream is to be something more than a delusion. A limit to population growth obviously exists—an objective analysis of available facts leads to no other conclusion. Should the limit be reached unexpectedly, " . . . irreparable injury will have been done to the social order." To voluntarily limit increasing consumption of raw materials and deterioration of the resource base is essential if we are to survive as a strong nation. Ordway's lucid essay is a significant contribution to the understanding of human population in relation to its resource base.

[1] Ordway, Samuel H., Jr. 1953. Resources and the American dream, including a theory of the limit of growth. 55 pp. New York: Ronald Press Co.

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Autecology of Microorganisms[1]

There are several books that can aid the student in the identification of yeasts, but to learn something of their biology one must go to the wide field of literature of mycology, food technology, brewing, physiology, medical mycology, etc. Ingram has brought together materials from these and other fields in which yeasts have been studied. As may be expected, this is largely a study in the biochemistry of the yeast cell. Because yeasts are used as a fundamental step in the brewing process, it is necessary that the important species be studied most intensively for the development of new strains more efficient in the production of alcohol, and that these be studied to learn more about the processes by which this alcohol is produced. It is important to know the function of each element and compound utilized by the yeast cell, so that more efficient combinations of elements and compounds may be obtained.

The subject of yeast biology is covered in a very thorough manner. As introductory material, the general morphology, cytology, and chemical composition of the yeast cell are presented. Fermentation is discussed from a historical point of view, and the chemistry of the process is developed for the principal mono- and multi-saccharides which yeasts are able to ferment. The effects of salts and vitamins on fermentation are considered. The several concepts of the chemistry of the fermentation process are explained and diagrammed. The Pasteur effect is discussed in the chapter on respiration. The strictly chemical portion of the book is concluded with chapters on carbon assimilation, nitrogen and sulfur metabolism, and on special aspects of yeast metabolism.

The chapter on growth is divided into two parts: under the chemical requirements for growth the roles of the major and minor elements, vitamins, and nutrilites are described; under the kinetics of growth the six principal phases of the life of yeasts are summarized under the headings of adaptation, lag, logarithmic, negative acceleration, stationary and death phases. Vegetative and sexual methods of reproduction, together with physiological requirements for such activity, are described. The genetics and variation of yeasts are considered, and suggested explanations of various phenomena described in earlier pages are given on the basis of Mendelian and cytoplasmic inheritance characters. The yeast colony in practice is discussed on the basis of different methods of producing yeast colonies and the types of variation in colonies. Finally there is a brief chapter on the ecology of yeasts.

As an example of a study in the autecology of a group of organisms, largely based on what is known about several intensely studied species, this book is a classic. Fifty tables, 42 text figures, and 12 plates illustrate the text and discussions, which are documented by about 280 references mostly published in the last twenty years.

The student of the synecology of yeasts will be disappointed in the brief chapter at the end of the book. The disappointment will lie not in the manner of presentation but in the paucity of material available for discussion. The chapter is largely a catalog of places where yeasts have been found: in air, water, soil, brine, flowers, honey, fruits, insects, milk, and elsewhere. Two species are considered as plant pathogens, several species as animal pathogens. A number of cases of symbiosis between yeasts and bacteria, fungi, and insects are mentioned. The role of yeasts in certain successions which have been studied is mentioned, but it is indicated that the mechanisms of the changes in populations are unknown. It is hinted, through analogy, that certain antibiotics produced by other organisms in the habitat have controlling influences.

It is obvious that very little is known about the role of the yeast in the community. It is apparent that mere enumeration of species in any particular habitat will not answer this question, nor will gross methods of isolation and study aid materially in giving an explanation.

[1] Ingram, M. 1955. An introduction to the biology of yeasts. xiii + 272 pp. New York: Pitman Publishing Corp. $5.00.

In this same vein one of the Methuen Monographs on Biological Subjects may be mentioned.[2] "The underlying theme of the monograph is none other than that known to all biologists as the *nitrogen cycle,* and an attempt has here been made to analyze some of the component steps of the cycle from the standpoint of the biochemistry of the various reactions and the microorganisms concerned." The ten chapters discuss, and the three plates illustrate, various phases of the role of nitrogen in the cells and metabolism of bacteria and fungi.

Many of the reactions described in these two books are basic not only to the organisms discussed but to all living organisms, although some of the reactions are restricted to the particular organism under discussion. A knowledge of biochemistry will aid the reader in understanding the more technical discussions, but the more important reactions are diagrammed or given in formulae so that it is not necessary to have a biochemistry text at one's elbow for translation of technical detail. As it becomes more and more important to understand the background of soil fertility, for instance, in the autecology of a wild or cultivated plant under study or a crop under cultivation, reference works such as these will become more and more important to the student of ecology.

[2] Fry, B. A. 1955. The nitrogen metabolism of microorganisms. ix + 166 pp. London: Methuen & Co., Ltd.; New York: John Wiley & Sons, Inc. $2.00.

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Three Publications from Western Lake Erie

During 1929 and 1930 a limnological survey of western Lake Erie (physical, chemical, plankton, and bottom organisms) was made; and in June 1933 a report was submitted to the Fish and Wildlife Service for publication. That report,[1] without being revised to take account of intervening publications, was issued in January 1955. It contains detailed tables, graphs, maps, and well-written discussion of the voluminous data collected. An "explanatory note" in the inside cover states that reports of this kind are "issued in processed form to avoid delay in publication."

From 1936 to 1955 Thomas H. Langlois was Director of the Franz Theodore Stone Laboratory situated near Put-in-Bay (South Bass Island) Ohio. In 1954 he published "The Western End of Lake Erie and Its Ecology."[2] After describing the physical environment (74 pp.) about 200 pages are devoted to the biota. This section is a sort of annotated check list of the species recorded for western Lake Erie by students and staff members (including class collections during summer field courses). Another 80 pages describe various methods of fish capture, followed by a 30-page "Summary and Discussion." A final section on "Fish Management" occupies the last 58 pages. The book contains extensive quotations from the literature, plus sections in which the author summarizes the work of others in his own words. Some errors have crept in. For example: table I (p. 28) purports to show "Weekly mean values of solar and sky radiation in langleys." On p. 27 the author states that "One langley equals one gram calory per square centimeter per minute," but on p. 29 he states that "gram calories per square centimeter" are langleys. The values in the table are in hundreds, and one who is familiar with the magnitude of solar radiation will recognize that they represent g. cal./cm.^{2}/day. Similarly on p. 363, Riley is credited with finding that "minimum phytoplankton production must lie between 0.32 and 2.17" in Linsley Pond. No units of any kind are associated with these numbers. Such errors could have been avoided if the author had invited editorial criticism from some of the scientists whose researches contributed to his book. The work suffers more, however, from rather arbitrary choice of subject matter and from failure to select, digest, evaluate and integrate available data into a coherent pattern of ecological relationships. The publishers have sabotaged the author's skillful photography by inferior reproduction.

James L. Verber, formerly a student at the F. T. Stone Laboratory, now associated with the Shore Erosion research program at Sandusky, Ohio, has compiled a "Bibliography of Physical Limnology 1781-1954."[3] It contains 44 pages of references and a useful index. Several papers of predominantly biologic interest are listed, and some contributions to physical limnology are missing. There are numerous errors in spelling but these will not interfere with the utilization of this list of references.

[1] Wright, S. 1955. Limnological survey of western Lake Erie. With chapters on the phytoplankton of western Lake Erie in collaboration with L. H. Tiffany, and the zooplankton of western Lake Erie in collaboration with Wilbur M. Tidd. U. S. Dep't of Interior, Fish and Wildlife Service. Washington, D. C. Special Scientific Report: Fisheries No. 139. 341 pp., 100 tables, 23 figs. $2.50.

[2] Langlois, T. H. 1954. The western end of Lake Erie and its ecology. Ann Arbor, Mich.: J. W. Edwards, Publisher, Inc. xx + 479 pp., 27 tables, 72 figs. $10.00

[3] Verber, J. L. 1955. Bibliography of physical limnology 1781-1954. Columbus, Ohio: State of Ohio Department of Natural Resources. 57 pp. Limited distribution, free to workers in the field.

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Pioneer Plant Geography[1]

Joseph Dalton Hooker was a botanical "giant," not merely of the nineteenth century, but of all scientific history. He was primarily a taxonomist whose research touched upon the floras of most of the world as they were known in his time. Major results of his work took the form of such publications as those on the flora of British India and the floras of Tasmania and New Zealand. The breadth of his taxonomic interest was shown particularly in the sweeping review of basic problems in plant relationships that appeared in "Genera Plantarum," in which he collaborated with George Bentham. The "timing" of Hooker's life and work was especially significant. Born in 1817, he was the second son of William Jackson Hooker, and grew up in an atmosphere of advanced scientific thought, under the influence of another great botanist, his father. Those were stirring times in the development of the broad field of natural history. Geologists were working out basic ideas on the mutability of continental outlines, seas, and land surfaces. Problems of biological speciation that had been troubling botanists and zoologists throughout the Renaissance were still unsolved, but were becoming more and more demanding because of the rapidly increasing knowledge of the world's plant and animal life.

In the midst of Hooker's career came the electrifying idea of natural selection, brought forward simultaneously by Wallace and Darwin, and amplified by the latter in so much carefully-thought-out and forcefully presented detail that it commanded immediate respect. Hooker quickly embraced the Darwinian ideas, and devoted a great deal of his own intellectual energy toward putting the ideas to use. He was in constant correspondence with the principal botanical students of his time, and was able thus to command an even larger mass of fact on the world's vegetation. Particularly notable was his long and productive acquaintance and correspondence with Asa Gray in America, who likewise readily accepted and used Darwinian theory.

Hooker was prodigiously productive of publications in his field, not only as a writer but as an editor. His writing was lucid, carefully organized, and easily read. He had no fear of the English language, and there were in his time no restrictions on the length of sentences and paragraphs. He was not troubled by our more modern dogma on the elimination of everything that is non-objective. His descriptions carry atmosphere as well as facts.

Throughout his many writings there are discussions of the basic phytogeographic problems that were being thought out in his time, and a few of his papers were primarily concerned with plant geography. Professor Turrill has gathered together the essential features of these writings into the present volume. The book consists largely of direct quotations, organized in terms of subject matter. There are ten chapters, the first of which contains some biographical details of Hooker's life, a list of his principal phytogeographic publications, and a short list of the foremost textbooks of plant geography published since 1872. Many of these texts deal with problems that either were first stated by Hooker or were elaborated by him. Chaper II deals with the distribution of arctic plants, and is based mainly upon a well-known paper on this subject published by Hooker in 1862. Chapter III is on his studies in Syria and Palestine. Chapters IV, V, and VI deal with India, Africa, and North America respectively. Chapter VII treats of papers on the flora of the Galapagos Archipelago, wherein Hooker reported on collections and observations by Darwin, Macrae, and other naturalists. Chapter VIII is on Antarctica, and contains Hooker's thoughts on the distribution of plants in the Southern Hemisphere. He had a great deal of personal knowledge of the island floras bordering the Antarctic, for he went with the exploring expedition commanded by Sir James Clark Ross in the ships Erebus and Terror. Chapter IX contains excerpts from miscellaneous writings: on the transmutation of species, on general problems of geographic distribution, and on various studies of island floras, particularly of those in the Atlantic. Chapter X contains Professor Turrill's general review of the works of Hooker as related to modern advances in taxonomy, speciation, and geographic distribution. The book concludes with an extensive bibliography of papers referred to in the text, and a subject index which includes references to species, genera, and families.

In each of the chapters Professor Turrill gives first the sources, in Hooker's papers, from which the ensuing excerpts are taken. At the end of each chapter is a brief but useful summary of later studies that have been made on the problems with which Hooker was concerned. Thus one can readily evaluate Hooker's views in terms of the realities as we now know them. In a surprising number of cases Hooker displayed that sure touch of genius that enabled him to arrive at conclusions that have never been superseded, even though he had to do this with what we now would regard as totally inadequate facts. He did not, of course, always succeed in accomplishing this. When he wrote his paper on arctic floras, knowledge of the floristic richness of the Beringian region was not at hand, leading him to center the development of arctic floras too much in northern Europe. On the other hand, his basic geographic organization of the flora of British India remains essentially intact.

The book is not one that can be read easily and continuously without a special knowledge of the world's floras —knowledge that very few people now possess—for the quotations in it contain voluminous discussions of species and genera. Not only must one have a modern knowledge of these details, but also a great deal of information about the way in which generic and specific concepts have changed since Hooker wrote. Nevertheless, the book contains a multitude of gems dealing with Hooker's botanical philosophy and the manner of his thought. These should be read and reread by students of plant geography, and by those taxonomists who make full use of plant geography as a tool of their trade.

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[1] Turrill, W. B. 1953. Pioneer plant geography; the phytogeographical researches of Sir Joseph Dalton Hooker. xii + 267 pp., 21 plates. The Hague: Martinus Jijhoff; and Waltham, Mass.: Chronica Botanica. (Lotsya—A Biological Miscellany, ed. F. Verdoorn, Vol. 4). $6.00.

Floral Ecology[1]

The floral ecologist of the golden age of Federico Delpino, Hermann Müller, Anton Kerner, Paul Knuth and Ernst Loew, from about 1870 to 1905, was a good general naturalist, interpreting every feature of the flower-animal relationship in terms of the Darwinian theory, and filling important gaps in knowledge, with regard to the sensory perceptions of animals and the effectiveness of floral characters as stimuli, with assumptions. In the era which followed Karl von Frisch's classical 1914 and 1919 papers on the honeybee many of these assumptions were replaced by experimentally verified knowledge. This line of investigations is still continuing actively in Germany under the leadership, among others, of Hans Kugler, the author of the book under review.

Kugler's Introduction to Floral Ecology is the first comprehensive general review of this field in fifty years. The contents of the work bear witness to the large advances which have been made in recent decades in the analysis of flower-insect interactions. Particularly valuable is the author's review of previously unsummarized material on flower colors, surface textures, odors, and forms as attractive stimuli in relation to the known perceptions and behavioral responses of flower-visiting insects. An interesting account is also given of wind pollination, which brings together the newer findings of Pohl on the comparative output and characteristics of pollen in wind-pollinated and insect-pollinated plants.

The second half of the book is devoted to a survey of various plant species, illustrating diverse floral mechanisms and modes of pollination. This account is organized according to a new ecological classification of insect-pollinated flowers, which seems to differ from the older classification of Kirchner, Knuth, Müller, and others, mainly in the fact that it emphasizes the general floral form rather than the agent of pollination. The major categories recognized are Disc flowers, Funnel flowers, Bell flowers, Salverform flowers, Lip flowers, Butterfly-like flowers, Head flowers, and Trap flowers. This reviewer personally prefers a modification of the simplest and also the oldest ecological classification of flowers, that of Delpino, which groups flowers according to their principal pollinating agent. The main groups, such as Bee flowers, Beetle flowers, Butterfly flowers, Moth flowers, etc., may be subdivided if desirable into Bumblebee flowers and Small bee flowers, etc., or combined into collective groups such as Bee and Long-tongued fly flowers or Promiscuous flowers.

In order to present as well-rounded a view of the subject as possible, Dr. Kugler has included an introductory section dealing with floral structures and mechanisms. Quite justifiably the author kept this section brief, since not a great deal new is added to the observations of the classical floral ecologists. The descriptions of Kerner in his well known "The Natural History of Plants" are still unsurpassed.

Dr. Kugler's bibliography of 471 entries possesses at once a strength and a weakness. Its strength lies in the rounding up of the German literature on floral ecology, which will be very useful for students of the field in English-speaking countries. The omission of important English and American papers on floral ecology by such authors as Robertson, Lovell, Clements, Arber and Parkin, etc., on the other hand, constitutes the weakness of the bibliography.

Throughout the book runs an implied but never explicitly stated agnosticism on the subject of adaptations. The word "Anpassung" is placed in quotation marks on page 53, and prefaced by a qualifying "nur" on page 88. The discussion of the correspondence between insect vision and flower colors and forms is conducted without reference to the concept of adaptation. This extreme caution is no doubt a reaction from the excessively speculative search for adaptations which prevailed in floral ecology a half century ago. It is also unfortunately true that there have been few experimental studies testing the adaptive values of floral characteristics. Where such studies have been carried out, however, as with Knoll's experiments on *Linaria* flowers with and without nectar guides exposed to visitations of the hawkmoth, *Macroglossum stellatarum*, they have frequently confirmed the hypothesis that the feature in question is adaptive. Such evidences are not emphasized by Dr. Kugler, nor are experiments suggested which in the future might enable us to evaluate the adaptive significance of floral characters in relation to pollination.

The study of the interrelationships between flowers and their pollinating agents is the meeting ground of a diverse lot of specialist fields, including systematic botany, floral morphology, entomology, ornithology, animal behavior, population genetics, and evolutionary biology. Dr. Kugler has competently reviewed the field up to the last two topics. The genetical and evolutionary aspects of flower pollination comprise two chapters in a general synthesis of floral ecology which still remain to be written.

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[1] Kugler, H. 1955. Einführung in die Blütenökologie. 278 pp., 240 figs., 10 plates. Stuttgart: Gustav Fischer Verlag. DM 28.— ($6.70).

Weeds[1]

"Strictly speaking, there are no species of weeds. Whether a plant . . . is considered a weed depends not only on its characteristics and habits, but also on its relative position with reference to other plants and animals." So, in his opening paragraph, the author adopts the ecological point of view which is maintained throughout.

The book consists of two parts. The first is on weeds and their control (without herbicides); the second is of 440 pages, 40 of which are devoted to a key, the remainder to nearly 600 species recognized as weeds. Glossary, literature references, and index follow in order.

For each weed are given the botanical and common names, life form, habitat, general distribution, origin, and flowering period. This is followed by an enumeration of key characters. Control measures are given last and very briefly. Considerable repetition is avoided by referring by number to other identical control measures.

Weeds and control measures of intensive agriculture

[1] Muenscher, W. C. 1955. Weeds. (2nd edn.) 560 pp. New York: Macmillan. $10.00.

are given almost exclusive attention. A number of the most undesirable species of the western ranges are not included. Among these are *Juniperus* spp., *Applopoppus* spp., *Chrysothamnus* spp., *Prosopis* spp., and *Actinea* spp.

Several *Artemisia* species are mentioned. However, the control recommended for big sagebrush, "Grub out the bushes and burn them," has scarcely any practical use. This species covers over 90 million acres of land, most of which is not worth paying taxes upon. Once big sagebrush is grubbed or plowed out, burning is not necessary to kill it. Burning without grubbing is a successful method that is fully described in the literature.

Halogeton glomeratus is one of the many species added in this edition. The common name "Barilla" is attributed to it, although Major in the Journal of Range Management 6(3): 187, pointed out that this name properly belongs to *Halogeton sativus* which has not yet been collected in the United States. While the description of *Halogeton glomeratus* is accurate, the control measures suggested, "Cultivation, hand hoeing, and harrowing" are utterly unrealistic. It would be as well to recommend mosquito abatement through use of the fly swatter. Is there evidence that Halogeton was introduced from Europe, as stated by the author?

Chemical control has been omitted from this edition because the material in the first edition was obsolete. Adequate treatment to include recent advances would have required too much expansion for one volume. In deleting the old material on chemical control, the author did not follow through to the references cited.

Only a few new references are included on chemical control. Most of these are proceedings of conferences which have doubtful status as publications, being for the most part mimeographed progress reports which have not been passed by an impartial editorial board.

By going to smaller print and omitting most of the material on chemical control from the first edition, 1935, the author has been able to add numerous species and several new plates while reducing the number of pages.

Much of the material in part one and some in part two would be useful to supplement the text in such college courses as elements of agronomy, economic botany, plant ecology, or weed control.

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California Grizzly[1]

This is the history of a hump-shouldered carnivore which weighed up to 1,200 pounds, measured from 6 to 10 feet in length, and could with one clout of his 13-inch paw stave in the skull of the mightiest Spanish bull. Despite his dominance over all other native animals, his abundance, adaptability, and continuous range from Oregon southward through California into northern Mexico, his survival was limited to about 300 years after man entered his domain. His trail in California was first intercepted during December, 1602, when Sebastian Vizcaino was at the site of Monterey; his tracks ended in and about Sequoia National Park in the early 1900's.

Before the invasion of Califronia by white men there was space for plenty of his kind along with the rather sparse population of Indians. With establishment of the first herds in mission days by the Spaniards, some of the animals found it easier to kill the cattle than to hunt wild food. Cattle were generally raised for hides and tallow, and the bountiful food supply furnished by the wasted meat bolstered the carnivore's population-numbers to an all-time high, perhaps close to 10,000. American travelers had some contact with the big animals, but with the gold rush the battle between man and carnivore became intense. His meat was food, and his pelt furnished rugs and beds. More important, however, miners and early farmers could not tolerate so large a carnivore, peaceful though he apparently was when not surprised or injured. Because of his size, temperament, and numbers, the settlers found him of great concern in their use of the California valleys and hills for farms, homes, and communities. He wandered into the outskirts of the new settlements, even to Mission Dolores in San Francisco in 1850. His numbers were a hazard to the travels and daily activities of the miners; they killed livestock and disturbed peaceful farmers; and for big game hunters he provided many surprises and much excitement—also injury and death. The improvement of rifles and other weapons gave the whites an ever-increasing advantage. Finally, as man crowded closer and closer together on his homeland, he was forced into oblivion. A half century after American occupation of his range, this great Carnivore—the California grizzly—was no more.

As stated by the authors on page 42, "The grizzly was a paradox. Attacked in the wild by man it was a dangerous and deadly adversary, yet some individuals taken into captivity became docile and trustworthy. When in search of animal food to satisfy its hunger, the bear would strike down any large beast; and in the fighting ring [where the Spaniards pitted them against wild bulls] it was a savage contender. . . . But when grizzlies congregated with their kind to relish some desirable food—clover, acorns, or whale—they ate together peaceably. If approached slowly and quietly by man, the bear would retire, unless it was a female with cubs. The grizzly had the power to be dominant but only exercised it when alarmed, disturbed, or injured; otherwise it was a well-behaved member of the animal community."

Although the California grizzly lived in the high mountains, he was primarily asssociated with the foothill regions where chaparral of many shrubby plants covered the slopes. On page 50 we read that, "Newberry (1857: 47-48) who was in the region northeast of Fort Reading, Shasta County, and around Lassen's Butte in 1855, said that the wide intervals between mature forest trees were covered by a 'dense growth of manzanita, ceanothus, and low scrub oak. These thickets . . . are intersected in every direction by . . . well-beaten paths' of grizzlies." The trails under the tangled branches provided shaded avenues to feeding, watering, resting and sleeping places. Manzanita and other plants afforded seasonal crops of berries, and on nearby slopes several species of oaks furnished acorns. Meadows afforded grasses, clovers, bulbs,

[1] Storer, Tracy I. and Lloyd P. Tevis, Jr. 1955. California Grizzly. 335 pp., 36 illustrations. Berkeley and Los Angeles: University of California Press. $7.50.

roots, and probably a fair supply of rodents and insects; all of these were utilized as food by the grizzlies.

This first comprehensive account of the California grizzly was written long after the grizzly's demise from that state. Consequently, as stated by the authors in the *Preface*, "This account must be historical and mainly from the written and published record, since the people who had firsthand experiences with the grizzly have also gone." Although Storer and Tevis say it is deficient in many respects, and readers will find ecologic information limited, an amazing wealth of data has been assembled, carefully analyzed, and presented in an interesting and readable manner. It is indeed a work well done!

In reading this historic account, I encountered only a few minor items that were detractive or questionable to me. On page 14 the authors state that while Sebastian Vizcaino was at Monterey, ". . . bears came down at night to feed on a whale carcass stranded on the beach. . . ." Reference to bears feeding on a whale carcass or marine animals washed ashore is repeated unnecessarily at least six times (p. 16, 23, 43, 60, 106 and 111). In discussing grizzly hunting, page 198, reference is made to Isaac Wistar who believed that the head shot was the surest and best way to shoot a grizzly. The authors then state that, "It is worthy of note that several skulls of grizzlies in the U. S. National Museum contain bullet holes; some hunters obviously held the same opinion as Wistar." I believe this has no significance, for I have seen many hunters shoot a bear or other big game animal in the head at gun-barrel distance for "good measure" or for "safety" purposes after it was downed by a shot in some other vital spot. In discussing grizzly habits on page 59, the authors state that bears killed and ate ". . . some horses. . . ." Again, on pages 120, 122, 171 and 173, they state that horses were killed by these large bears. In southwestern Yukon Territory, where grizzly bears are still common, I was informed by guides and other residents that these bears inflict high mortality to cattle on open ranges, but horses are wintered in the same valleys where grizzlies occur regularly and no deaths have been attributed to the bears. The evidence concerning the California grizzly's gustatory proclivities for human flesh is more confusing than convincing. On page 58 the authors quote Mills (1919) as stating that, "No grizzly ate human flesh. . . ." On page 88 the authors claim that the Wintun and Yurok Indians believed that bears devoured Indians, and on page 214 they state that, "Although grizzlies tore and mangled many victims, curiously they did not eat them. At least, only one report of a grizzly eating human flesh has come to our attention." Finally on page 262, a quotation from the Red Bluff *News* concerning a famous grizzly was reprinted in the Sacramento *Daily Union* for June 21, 1889, and states that, "Hundreds of cattle, sheep, hogs and human beings have fallen victims to his appetite. . . ." That these items are few and minor is certainly very creditable to the authors when one considers the difficulty they faced in screening and analyzing a wide volume of published, written, and reported material.

This book will not only serve as a reference and source of information for biologists, historians, and others interested with California, it should instill humility in those who worry not about increasing our own numbers and who do not value wild things that are now our heritage. How many species shall take places of extinction beside the California grizzly before we learn to direct the hand of man less violently, more compassionately?

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North American Moose[1]

Numerous reports have been published on the description and habits of the moose, and a few ecologic studies of moose are in print. Peterson's report brings together findings from many published reports and presents his Ontario studies started in 1946. As stated by the author on page 4, ". . . it is merely a preliminary report on our present state of knowledge of this animal, for studies are under way which will enlarge our understanding of certain factors, fill in existing hiatuses of knowledge, and modify some of the concepts expressed here."

The reader will be impressed with how little is known today about the "inside" workings of a moose population. This can be attributed to the fact that scientific studies of wildlife are only about two decades old, and that large, thinly populated animals like the moose do not provide data in volume similar to those gathered from small, densely populated animals. Peterson's book contains only 18 pages on population studies, and these are devoted almost exclusively to counts of moose.

In chapter 8 on the rate of reproduction, Peterson states that, "The reproductive rate of moose is greatly affected by there being a high proportion of so-called barren cows." As a wildlifer I have an aversion to the term "barren." To me it implies sterility or incapacity to produce offspring. How often is this actually the case when this term is used in big-game parlance? Examination of the data in Table V and those cited from literature on page 58 do not show whether the variable pregnancy rates reflect study techniques or whether moose actually show such wide variability in pregnancy rates. Before reproductive rates in moose become meaningful, it will be necessary to determine what effects density and nutrition have on fertility (including breeding age and pregnancy rates), natality (including twinning), and mortality rates.

Chapter 12 presents an "Annotated list of the principal moose food plants of eastern North America." The list is divided by an artificial system into "Trees and Shrubs," "Aquatic and Semi-aquatic Plants," and "Other Plants." The plants in each group are then arranged taxonomically and treated singly. I would prefer to have the plants arranged by some artificial system such as order of use, or to have them grouped by associations. The advantage of such presentations is suggested by Peterson's statement on page 125: ". . . the availability of a food species is more important in influencing the actual composition of the diet than palatability or individual preference." Again, on page 146 the author refers to McMillan's[2] summer food-habits study in the Yellowstone National Park area

[1] Peterson, Randolph L. 1955. North American Moose. 280 pp., 65 figures, 35 tables. Toronto: University of Toronto Press. $12.50.

[2] McMillan, J. F. 1953. Some feeding habits of moose in Yellowstone Park. Ecology 34: 102-110.

where about 88 percent of the food consisted of browse from two species of willow. *Salix Geyeriana* was eaten about three times more frequently than *S. Wolfii*. McMillan states: "The fact that *S. Geyeriana* is tall enough in many places to hide the moose while feeding may account for part of the difference in frequency of utilization." An association might contain tall plants that show *no* food value but serve as valuable cover while moose are feeding on other plants in the same association.

In discussing the distribution and status of moose in Ontario, p. 51, Peterson points out that, "While the steady increase in estimated numbers over this period undoubtedly represents, in part, an actual increase in the total population, the fact remains that a significant portion of this increase represents a more accurate knowledge of existing populations." In all probability this observation applies to the reported population estimates of moose given on page 27 for Minnesota in 1948 (1,100 moose) and on page 29 for Idaho in the same year (1,000 moose). I would question that there were more moose in Minnesota in 1948 than occurred on Idaho's extensive and rugged ranges that year.

Applendix A is an 18-page chapter on "A study of mandibular tooth-wear as an index to age of moose" by R. C. Passmore, R. L. Peterson, and A. T. Cringan. Appendix B is a seven-page chapter on "Studies of moose antler development in relation to age" by A. T. Cringan. These two chapters are valuable additions to the publication.

The book is written in a pleasing, simple, straightforward style; but the reader may have to pay what seems an excessive price to enjoy it.

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Water[1]

The purpose of the new Yearbook of Agriculture "is to explain the nature, behavior and conservation of water in agriculture." It is purported to be nontechnically written for "farm people and those interested in rural living." However, by its very nature, discussing a compound which is a basic essential of life, the book transcends these relatively narrow limits of interest and should prove to be of value to every biologist. Many of the 96 chapters will be intelligible only to a trained biologist.

The book is not intended to convey details of new research, but rather to present brief but comprehensive surveys of our knowledge of various aspects of water. The individual chapters vary from 2 to 21 pages in length. Only one third of the chapters contain lists of publications "for further reference." These lists are, regrettably, very brief.

Among the chapters which will be of most interest to ecologists are: From ocean to sky to land to ocean (the water cycle), by William C. Ackermann, E. A. Colman, and Harold O. Ogrosky; Fog, mist, dew and other sources of water for plants, by F. W. Went; The possibilities of land treatment in flood prevention, by Howard O. Matson, William L. Heard, George E. Lamp, and David M. Ilch; Frozen soil and spring and winter floods, by Herbert C. Storey; Fire on the watersheds of the nation, by C. Allan Friedrich; Trees also need water at the right time and place, by G. L. Hayes and Jesse H. Buell; How to get more snow water from forest lands, by B. C. Goodell and H. G. Wilm; Managing forests to control soil erosion, by E. G. Dunford and Sidney Weitzman; Climate as an index of irrigation needs, by Harry F. Blaney; The water budget and its use in irrigation needs, by C. W. Thornthwaite and J. R. Mather; How to measure the moisture in the soil, by Howard R. Haise; Phreatophytes—a serious problem in the West, by Herbert C. Fletcher and Harold B. Elmendorf; and Development and improvement of coastal marsh ranges, by Robert E. Williams.

Only one chapter contains material which is not consistent with the general high standard of the new Yearbook. This chapter, "The age-old debate about a forked stick," was written by a self-styled, spare-time waterdowser. While the intent of the author allegedly "is to tell both sides of the dowsing question without trying to convince the reader one way or the other," the text is definitely slanted and prodowsing. This, of course, in the eyes of many who receive copies of the Yearbook, will lend support to the claims of water-witches and raises the question, "Does the United States Department of Agriculture now endorse water dowsing?"

The new Yearbook is attractively bound in heavy cloth, lithographed and overprinted with an attractive design, and is very reasonably priced—at perhaps a fourth of its cost had it been published commercially. "Water" should be added to the library of every ecologist as a basic source book.

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[1] Water. The Yearbook of Agriculture 1955. xiii + 751 pp. Washington: The United States Department of Agriculture. Available from: Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C. $2.00.

A Bibliography of Scientific and Technical Glossaries[1]

This excellent compilation, the first in its field, and in the same format as the author's earlier "Bibliography of interlingual scientific and technical dictionaries," will at once find a place on the shelves of all scientists who feel obliged to have at hand an access to literatures outside those of their immediate competence and geographic concern. In this respect it has both indirect and direct value to ecologists.

Indirectly, it serves as a practicable reference volume of the glossaries in all fields of science. Full particulars are given for 1558 publications, printed in 27 different languages, and representing the standardizing organizations of many countries. Entries are grouped by the Universal Decimal Classification. The summary of the headings indicates at once that this type of intellectual activity is far more highly developed in the "applied sciences" than in the "natural sciences." Indeed, there was no reason to subdivide "botany" and "zoology," for which there are only three and five entries respectively. Forestry, agriculture and related fields merit over 50 entries, only one of which is in the English language, and the majority of which concern agricultural machinery. The same type of relative emphasis is evident in the lists of "author organizations," arranged by country. For the United States there are 7 entries, all of which relate to engineering and technology. Although there are undoubtedly a large number of glossaries prepared by individual scientists, it is curious and interesting that Mr. Wüster found no others that would come under his concept of "national standards," such as sponsorship by a scientific society presumably would give.

[1] Wüster, Eugen. 1955. Bibliography of monolingual scientific and technical glossaries. Volume 1: National standards. Bibliographie de vocabulaires scientifiques et techniques monolingues. Volume 1: Normes nationales. (Bilingual.) 223 pp. Paris: United Nations Educational, Scientific and Cultural Organization. $2.50 (from UNESCO Publications Service, 475 Fifth Ave., New York 17).

Directly, this publication offers a challenge to, and reveals a need by, the membership of the Ecological Society of America. Ecology as a scientific field has the reputation for terminologic complexity and redundancy. Yet there has been no established glossary, even for a basic minimum of terms. It is true that attempts have been made in this direction. One such manuscript was actually under consideration recently by a Committee of the Society, with sailing that was not smooth—an event which should not discourage us from a new attempt.

Any serious consideration of a glossary for ecology, such as would satisfy the standards of this UNESCO volume, will bring to the open, and force a decision upon, a problem as yet unsolved in the thinking of many ecologists. On the one hand, there will be the "encyclopaedists," who will want a full listing of terms from soil science, meteorology and other natural sciences that are concerned with factors of the environment and with those "interrelationships" by which the science of ecology is so often defined. To these will be added the terms of the applied ecologies, including forestry, wildlife management and even agriculture. It is a sober and serious question as to how this policy can be rationally circumscribed so that its extent does not become synonymous with the entire field of natural science, pure and applied. Perhaps however it should be so synonymous. On the other hand, there will be those students of plant and animal communities who consider that they have a distinctive and separable subject matter, the study of which can be rationally segregated from the other natural sciences, with a vocabulary of its own.

Regardless of which direction these intra-Society problems may take, the challenge of a standardized glossary for ecology is one that calls for early attention, all the more so now that we see the glaring absence of its kind in the volume here reviewed.

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